Vol. 109. Part 2. Pp. 65–110. 11 figs. 15th June, 1957

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ROYAL ENTOMOLOGICAL SOCIETY

OF

LONDON

World List abbreviation: *Trans. R. ent. Soc. Lond.*

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WILLIAMS, J. R. The sugar-cane Delphacidae and their natural enemies in Mauritius . . 65—110, 11 text-figs.

LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7.

Price 16s. 0d.

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THE SUGAR-CANE DELPHACIDAE AND THEIR NATURAL ENEMIES IN MAURITIUS.

By J. R. Williams.

(*Entomologist, Mauritius Sugar Industry Research Institute, Réduit, Mauritius*).*

Manuscript received 17th August, 1956.

(Read 5th December, 1956).

With 11 Text-figures.

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I. Introduction.

Until recently comparatively little attention had been paid in Mauritius to the sap-sucking insects of sugar-cane for, with one or two exceptions, they cause no obvious injury to the growth of the crop. The sugar industry of the island has also only recently become concerned about certain important diseases of sugar-cane which are, or may be, transmitted by insects. In 1953 Fiji Disease of sugar-cane appeared in the cane plantations along the east coast of Madagascar, and fear that it might find its way to Mauritius focused attention upon the presence of the Delphacid *Perkinsiella saccharicida* Kirkaldy, a known vector of the disease. With the realisation that this leafhopper had become potentially important as a vector of the Fiji Disease virus, it became desirable to study its bionomics with the object not only of obtaining an appreciation of its abundance and distribution, but also of determining the factors which regulate the density of its populations and the possibility of augmenting those factors. The present study was undertaken primarily for this purpose. A wider interest in sap-sucking insects has also arisen because certain established diseases of sugar-cane, which may be insect-borne, are now of considerable importance in Mauritius. These are Chlorotic Streak and Ratoon Stunting diseases, respectively. Attempts have been made to obtain transmission of the former with the leafhoppers dealt with in this paper.

II. The Species and Their Biology.

The Delphacid leafhoppers found on sugar-cane in Mauritius belong to three species. These are *Perkinsiella saccharicida* Kirkaldy, *Dicranotropis muiri* Kirkaldy and *Peregrinus maidis* (Ashmead). The biology and bionomics of the two former species, which are true sugar-cane insects in the sense that they breed habitually upon this plant, are the subjects of the present paper.

P. maidis is in a different category. It is the cosmopolitan maize leafhopper which seems to be confined to maize for its development. Adults have,

however, occasionally been caught on sugar-cane at some distance from plantations of maize. In the laboratory the adults feed and oviposit very readily when confined on sugar-cane but the newly-hatched nymphs do not survive. The few adults found on sugar-cane in the field are macropterous and are obviously to be regarded as strays which may feed on cane and perhaps also oviposit before migrating further. It should, however, be noted that the eggs of *Peregrinus* were never found in sugar-cane in the field. Apart from maize and sugar-cane, adults of *Peregrinus* were occasionally seen on *Coix lachryma-jobi* and *Pennisetum purpureum*. Its eggs were also found in the latter.

Peregrinus is referred to again only in the section on descriptions and incidentally as an alternate host of some of the parasites of *Perkinsiella* and *Dicranotropis*.

1. Historical.

Perkinsiella saccharicida Kirkaldy (1903) is a sugar-cane insect well known from the writings of Hawaiian entomologists. Zimmerman (1948) may be consulted for a summarised account of the insect in Hawaii and for references to important Hawaiian publications, while Metcalf (1943) gives a complete bibliography of the many publications dealing with the species up to 1940.

P. saccharicida is considered to be of Australian origin (Zimmerman, 1948), and the world distribution given by Box (1953) is as follows—Queensland, Hawaii (accidentally introduced from Queensland), Formosa (accidentally introduced from Hawaii), Java, Mauritius and Natal. To this list of countries may now be added Réunion Island, where the insect was collected by the author in 1951 (Williams and Mamet, 1954), and Madagascar, where the author collected it at several localities along the east coast and also at Ambanje and Nossi Bé in the north-west in 1954. Hall (1955) has since recorded it from Madagascar where it has assumed considerable importance owing to the outbreak there of Fiji Disease of sugar-cane.

Muir (1926) was apparently the first to record *P. saccharicida* from Mauritius. Swezey (1936) also recorded it from the island and Vinson (1938), after searching cane fields, verified these records and stated that adults were comparatively rare and could only be found after patient search; he also noted the occurrence of parasitism by an undetermined Dryinid.

Dicranotropis muiri Kirkaldy (1907) was described from specimens collected in South China (Muir, 1916) and it was subsequently recorded from Formosa, Luzon (Philippines), Java and Borneo (Muir, 1917). The leafhopper was first collected in Mauritius in 1954 by the author and during the same year it was also found by him on sugar-cane in Réunion Island and at several places in Madagascar (Williams, 1956*a*), namely Ambanje and L'Alaotra in the north-west and centre of the island, respectively, and at Brickaville and Ivondro along the east coast.

It is, perhaps, surprising that *D. muiri* had not previously been collected on sugar-cane in Mauritius. It has, however, already been mentioned that cane leafhoppers have only recently attracted attention and, as the insect is inconspicuous to the casual eye, the " egg spots " which are often common on cane leaves had been all attributed to *P. saccharicida*. The Fulgoroidea of the island have also never been systematically collected and the Mauritian representatives of this group are still virtually unknown.

It may be assumed that both *P. saccharicida* and *D. muiri* are alien species originating from Oriental or Australasian regions and that they were at some time introduced into Mauritius with importations of sugar-cane. Their presence in Réunion Island and Madagascar may be accounted for similarly, although, owing to exchanges of cane varieties between these three islands, it is uncertain if the two species were introduced into each direct from Eastern countries or if the insects, after becoming established in one, were later passed to the other islands.

Sugar-cane appears to have been first introduced into Mauritius by the Dutch from Java in 1639 (Merle, 1950). Subsequently, in the eighteenth and nineteenth centuries, other importations were made from the East Indies, Australia, the South Pacific and elsewhere (Sornay, 1920; Deerr, 1921). A stimulus for such importations was provided in the middle of the nineteenth century by the failure, owing to disease, of the Otaheite variety which was then the principal cane cultivated. As a result of the considerable importations which were made (Earle, 1928), Mauritius, in fact, became for a while a centre for distribution of cane varieties. There is ample evidence that little or no attention was given in former days to the dangers of inadvertently introducing insects with consignments of sugar-cane. The insect fauna of Mauritius, which is reasonably well known (Williams and Mamet, 1954), consists overwhelmingly of alien species and is testimony to the ease with which pests enter even an isolated, oceanic island when phytosanitary practices are inadequate or absent. Evidently, the date or dates of the introduction of *P. saccharicida* and *D. muiri* into Mauritius cannot be fixed even tentatively but, on the other hand, it is clear that both insects may have existed unnoticed in the island since the early days of cane cultivation. It is also not improbable that the two species reached Réunion Island and Madagascar via Mauritius.

2. Descriptions of the Immature Stages.

The following descriptions are designed to enable the various immature forms of *P. saccharicida*, *D. muiri* and *Peregrinus maidis* to be distinguished from each other. The descriptions of the nymphs are therefore not exhaustive and concern only selected characters. *Peregrinus* is included because an ability to distinguish its eggs and nymphs quickly from those of *Perkinsiella* and *Dicranotropis* is important in field studies.

(*a*) The eggs.

The eggs of the three species are of similar shape, as shown in figure 1. The chorion is smooth, shiny and tough. It becomes rather brittle in the older eggs. The eggs swell a certain amount after deposition, while before eclosion their outline often becomes irregular owing to bulging caused by the embryonic nymph. The curvature of individual eggs varies to some extent. The anterior ends of the eggs possess a cap which is unoccupied by the embryonic nymph and which breaks away during eclosion. The chorion of the cap is thicker than that over the rest of the eggs. Oviposition occurs into incisions made by the ovipositor in the tissues of the host-plant. The anterior ends of the eggs are either flush with the surface of the tissues in which they are embedded or they project slightly.

The eggs of the three species are easily distinguished. Those of *Dicranotropis* are laid singly, and after deposition the exposed cap is covered by the female with a secretion which hardens to form a thin, transparent, film invisible to the naked eye. The cap has a strong chorion and is flattened or indented at its extremity ; it fits snugly into the hole in the surface of the cane tissues. The length of the eggs is about 0·85 mm. when freshly laid and about 0·95 mm. before eclosion.

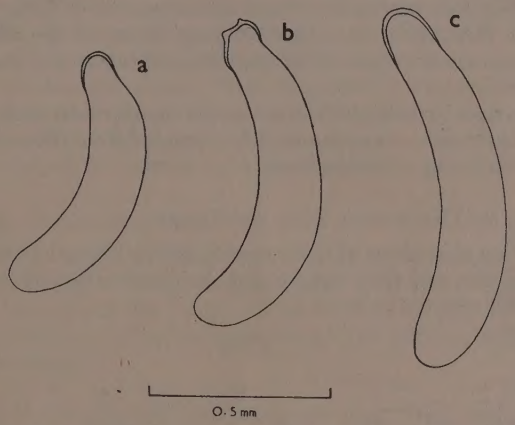

FIG. 1.—Freshly laid eggs of (*a*) *Peregrinus maidis* (Ashm.). (*b*) *Dicranotropis muiri* Kirk. (*c*) *Perkinsiella saccharicida* Kirk.

The eggs of *Perkinsiella* and *Peregrinus* are usually laid in batches of three to five. The eggs of each batch lie in a single row in a slit made by the ovipositor of the female. The slit-like incisions, and therefore the rows of eggs, are always parallel to the vascular strands of the host-plant. The exposed caps of the eggs are flattened laterally as if pinched at the tips and they may or may not project a little from the plant tissues. A fluid, which soon solidifies, is deposited by the females over the exposed ends of the eggs but, unlike the secretion of *Dicranotropis*, it hardens to form a white, bulky, mass which is very obvious to the naked eye. The eggs of *Perkinsiella* and *Peregrinus*, although otherwise similar, are of very different size. The former are about 1·0 mm. long when freshly laid and about 1·15 mm. long before eclosion. Those of *Peregrinus* are about 0·7 mm. and 0·82 mm. long when freshly laid and before eclosion, respectively.

(*b*) The nymphs.

The more evident changes which occur during nymphal development concern body size, pigmentation, growth of wing pads, sensorisation of the antennae and leg structure. It is not necessary to consider all these characters to determine the instar to which a nymph belongs. Most of them are, in fact, unsatisfactory for this purpose. Thus, all parts of the body, excluding appendages, increase in size during instars so that their measurements cannot be used as characters to identify any instar. Pigmentation differences between instars are not always pronounced or consistent, while wing pads appear as distinct structures only in the third instar. A definite character which differs in each

instar is presented by the antennae ; this is the number of sensoria on the second segment. However, it is a matter of considerable difficulty to count these sensoria so that the practical value of this character is small. The legs provide the best characters for separating the instars. Their segments are rigid structures with dimensions which do not vary during an instar. Measurements of convenient leg segments may therefore be used to characterise the various instars of a species. In addition, as far as the species considered here are concerned, the metathoracic legs possess structural characters which differ in each instar but which are identical in the corresponding instars of the different species. These characters are the spinosity of the tibia and tarsus and the segmentation of the latter.

The species may be distinguished in the nymphal form by their pigmentation. The nymphs of *Peregrinus* are also readily separated from those of *Dicranotropis* and *Perkinsiella* by leg measurements.

(i) *Structure of the Metathoracic Tibia and Tarsus.*

The following characters of the nymphal hind tibia and tarsus are common to the three species and they serve to enable identification of the instars. The characters are illustrated in figure 2.

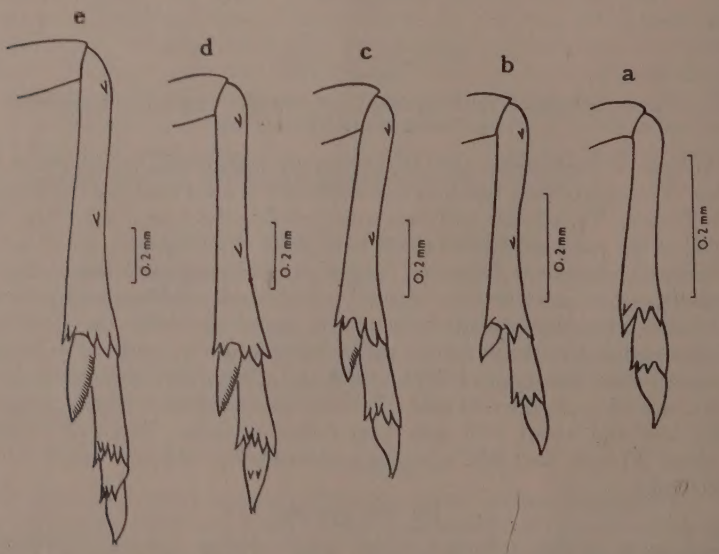

Fig. 2.—*Dicranotropis muiri* Kirk. (*a*)–(*e*) Metathoracic tibia and tarsus of first to fifth nymphal instars, respectively.

First instar.—The tibia has four spines or spurs distally on the ventral side, one of which is much larger than the others and is destined to become the articulated, mobile, spur of subsequent instars.[1] The tarsus is bisegmentate,

[1] Kirkaldy (1906) was incorrect when he stated that the first nymphal instar of *P. saccharicida* has a *mobile* spur on the hind tibia.

the first segment bears four spines distally on its ventral side, while the second segment is spineless and bears the pretarsus consisting of two claws and a median arolium.

Second instar.—The large tibial spur is articulated, while a small spur is present near the proximal end of the tibia and another midway along its length.

Third instar.—The mobile tibial spur bears a small row of spines along its edge, while the number of non-articulated spurs which accompany it has increased to five. The first tarsal segment has five spines distally.

Fourth instar.—The row of marginal spines on the mobile tibial spur has enlarged so as to form a serrated edge. The first tarsal segment bears six spurs distally (occasionally seven), while the second tarsal segment has one to three, usually two, small spines midway along its length on the ventral surface.

Fifth instar.—Three tarsal segments are present. The first bears seven spines distally, the second bears four, while the third is spineless.

(ii) *Length of the Metathoracic Femur.*

The hind femur is a convenient segment for measurement because of its simple cylindrical form. It is seen from Table I that the measurements for the successive instars conform to Dyar's Law. The nymphs of *Dicranotropis* and *Peregrinus*, which are of similar appearance when young, are easily separated by these measurements.

TABLE I.—*Lengths of nymphal hind femurs in mm.* (*All measurements taken along leading* (*anterior*) *side of femur to the nearest micrometer unit of* 0·016 *mm. Means derived from twenty femurs from different individuals*).

	D. muiri.			*P. maidis.*			*P. saccharicida.*		
	Mean.	Max.	Min.	Mean.	Max.	Min.	Mean.	Max.	Min.
1st instar .	0·194	0·208	0·176	0·142	0·144	0·128	0·195	0·208	0·176
2nd ,, .	0·271	0·288	0·256	0·192	0·208	0·176	0·293	0·320	0·256
3rd ,, .	0·390	0·416	0·368	0·264	0·288	0·240	0·419	0·448	0·384
4th ,, .	0·531	0·592	0·480	0·362	0·400	0·336	0·599	0·624	0·560
5th ,, .	0·749	0·784	0·720	0·518	0·544	0·480	0·823	0·864	0·768

(iii) *Pigmentation.*

The freshly-emerged nymphs of the three species are very similar, being of a creamy-white colour with red eyes. Pigmentation becomes apparent later during the first instar but it is often slight and ill defined; it becomes more pronounced, and its pattern better defined, as the nymphs pass through their successive instars. Except sometimes for spirit-preserved first instar nymphs, all the stages of *Perkinsiella* are easily separated from those of *Dicranotropis* and *Peregrinus* by differences of pigmentation. The young nymphs of the two latter species are not always easily distinguished from each other by pigmentation differences alone.

Dicranotropis.—Soon after hatching the nymph assumes a general yellowish hue which is more pronounced in some individuals than in others. The yellow colour is often more intense dorsally. Light brown patches are often discernible on the head, thorax and abdomen and they are most distinct, and usually present even in the least pigmented individuals, upon the dorsum of the first

two abdominal segments and upon the dorsolateral areas of the thoracic segments.

In subsequent instars the light brown areas become more extensive on the dorsal surface of the body, so that the nymphs acquire a mottled appearance. The basic, general, colour remains a straw-like yellow. The ventral surface of the body, as well as the legs and antennae, is without brown pigment.

Peregrinus.—The nymphs, like those of *Dicranotropis*, are of a general yellow colour. In the first instar very faint brown pigmentation may be evident on the dorsal surface of the thorax and abdomen. The pigment is distributed uniformly on the sclerites, there being no spots or patches.

In the second instar the pigmentation is more evident and the abdominal tergites are uniformly light brown. In the later instars small patches of darker brown appear at the lateral ends of the posterior tergites and at the spiracles. The thorax is faintly mottled in the fifth instar. The ventral surface of the body, the legs and the antennae are, like *Dicranotropis*, without dark pigment.

Perkinsiella.—The first instar nymphs are whitish, with the frons, lateral to the keels and between the sense organs, light brown to fuscous. Some individuals also have small fuscous patches over the body.

In the second instar fuscous areas are present on the frons, clypeus, dorsolaterally on the metathorax, and laterally on the posterior three or four abdominal tergites. Fuscous patches may also be present on the legs and other parts of the body, while the antennae are also of a brown colour.

In subsequent instars pigmentation is conspicuous even to the naked eye. The pigment becomes very dark and its pattern more variegated. The whole dorsal surface presents an intricate pattern of dark pigmentation. The antennae and clypeus are dark and the legs have conspicuous brownish-black patches. The vertex and the upper part of the frons is pigmented but the lower part of the frons is not.

3. Life Histories and Habits.

The life history and biology of *P. saccharicida* has already been adequately described in most respects (*vide* Metcalf, 1943; Zimmerman, 1948). The following account is therefore brief and chiefly concerned with local observations.

The biology of *D. muiri* has never been previously described. Its life cycle and habits are, however, very similar to those of *P. saccharicida* and, except when stated otherwise, the following account applies to both species.

(*a*) Oviposition.

Some description of the manner in which the eggs are laid has been given above.

The females may oviposit at any time, although they do so mostly at night. The incisions made in the cane tissues by *Dicranotropis* are small and designed for one egg, those of *Perkinsiella* are slit-like and follow the direction of the vascular strands and they usually receive several eggs.

Oviposition occurs chiefly into the thicker parts of the leaf blade, the upper (inner) surface of the mid-rib being the favourite site. Otherwise, eggs may be laid in the leaf sheath when this is not densely pubescent. Zimmerman (1948) states that the eggs of *P. saccharicida* are also laid in the stalk internodes.

This was not observed in Mauritius although it may well happen occasionally. When the eggs are laid in tissues which have a thickness less than the length of the eggs, *e.g.* a leaf mid-rib or leaf sheath of very young cane shoots, the ovipositor is inserted obliquely so that the eggs lie with their sides against the epidermis.

The incisions in the cane tissues made during oviposition frequently serve to allow entry of the Red Rot fungus (*Physalospora tucumanensis* Speg.), and the characteristic reddish discoloration of the invaded tissues around the incisions (the " egg spots ") enables oviposition sites and the location of leafhopper infestations to be detected readily in the field.

(*b*) Emergence.

The emerging nymph pushes off the cap of the egg and displaces the hard protective secretion which closed the egg cavity. It then slowly works its way out of the egg shell, swaying slightly to and fro, until it is perpendicular to the cane tissues and held only by the tip of its abdomen. The appendages are then freed and emergence is completed. The embryonic membrane remains projecting noticeably from the empty egg. There were very few instances of unsuccessful emergence during laboratory breeding.

(*c*) Nymphal and adult habits.

Both nymphs and adults are essentially nocturnal and during the daytime they conceal themselves on various parts of the cane plants and also among dead, decaying leaves lying on the soil (the cane " trash "). The nymphs favour moist, shady, places more than do the adults and they are consequently found mostly in the lower strata of cane growth, where they tend to congregate in certain sites, *e.g.* at the base of stalks amid moist leaf trash, under leaves which trail over the soil, inside semi-detached leaf sheaths, etc. The adults commonly frequent other places where nymphs, especially the younger ones, are seldom found. Adults of *Perkinsiella* hide to a large extent in the funnel-like cavity formed by the bases of the newly-opened leaves of the crown, otherwise they often rest on the stalks and leaf sheaths. The adults of *Dicranotropis* prefer the under surface of the open leaf blade and are not often found in the funnel of the crown. These concealment habits of the adults of the two species are so distinct that their collection, in a field where neither is very abundant, often necessitates the use of different techniques. Thus, in a field of moderately grown cane, adults of *Perkinsiella* are most easily obtained by searching the funnels of the crowns, while adults of *Dicranotropis* are best sought by squatting amid the cane and looking up at the under surfaces of the leaves. It seems worth remarking that these differing adult habits of the two species may be correlated with their pigmentation. *Perkinsiella* is a dark insect and is conspicuous on an open background but *Dicranotropis*, on account of its yellowish or pale straw colour, merges extremely well into a green background, particularly in sunlight on the under surface of a translucent leaf blade.

The injury done to cane plants by the nymphs and adults consists of (*a*) removal of plant juices during feeding, and (*b*) mechanical injury to tissues during oviposition. The Red Rot fungus usually invades tissues damaged during oviposition.

(*d*) Other food-plants.

No food-plant other than sugar-cane was found despite sweepings of grasses and other low vegetation around cane fields and elsewhere. Careful examination of larger grasses such as *Pennisetum purpureum* and *Panicum maximum* was also fruitless. Both species have, in fact, been seen only on sugar-cane and at light. Pemberton (1919) in Hawaii reports finding *P. saccharicida* breeding on *Paspalum conjugatum*, " Hilo " grass, and on five other undetermined grasses and three sedges.

Both species will feed and oviposit on maize when confined with this plant in the laboratory, but only with reluctance and they do not survive.

(*e*) Duration of the life cycles.

The duration of development from egg to adult was determined in the laboratory on young potted plants during the hot season (average room temperature about 25° C.). The development of *Perkinsiella* was usually completed within 45–50 days after oviposition, while the development of *Dicranotropis*, the smaller of the two species, averaged a few days less. The egg stage of both species lasted between 11–15 days.

(*f*) Alary polymorphism.

Alary polymorphism is common in the Delphacidae and three main forms may be distinguished. These are the macropterous form, which has fully-developed tegmina extending beyond the tip of the abdomen; the brachypterous form, which has abbreviated tegmina with reduced venation ; and the apterous form. Only the macropterous form has fully-developed hind wings and the ability to fly. The term koeliopterous is sometimes applied to those brachypterous forms where the tegmina are not excessively reduced but instead cover the greater part of the abdomen, or just cover it completely, and have the apical cells moderately developed.

Kirkaldy (1906) and all subsequent authors, with one exception, state that *P. saccharicida* is dimorphic, with macropterous and brachypterous forms, in the female sex only and that males are always macropterous. Imms (1942) quotes *P. saccharicida* as an example of an insect polymorphic in one sex only. Giffard's solitary record (1922) of brachypterous males is stated by Zimmerman (1948) to be " evidently in error ". It is, therefore, of particular interest that macropterous and brachypterous forms of both sexes occur in Mauritius. The brachypterous males and females have the tegmina abbreviated to the same extent and they conform to the definition of koeliopterous given above.

Polymorphism in *D. muiri* is not recorded in the few published works which mention this species. In Mauritius, the insect is dimorphic and, as with *Perkinsiella*, has macropterous and koeliopterous forms in both sexes.

Dimorphism is a constant feature of both species in Mauritius, the macropterous and koeliopterous forms being found together throughout the year in all cane-growing regions. To gauge the relative abundance of these forms, collections of adults were made in the same locality over the greater part of a year. The locality chosen was at about 500 feet altitude and was representative of conditions between the climatic extremes for cane cultivation in the island. The results of the collections are given in Tables II and III. The

TABLE II.—*Alary polymorphism in* P. saccharicida.

Month.	Females. Number collected.	Females. % koeliopterous.	Males. Number collected.	Males. % koeliopterous.	Males and females. Number collected.	Males and females. % koeliopterous.
1955						
July .	173	59·5	113	8·0	286	39·2
Sept. .	36	58·3	14	14·3	50	46·0
Oct. .	124	33·1	64	7·8	188	24·5
Nov. .	63	11·1	37	2·7	100	8·0
Dec. .	82	15·9	27	3·7	109	12·8
1956						
Jan. .	.	.	.	.	315	12·4
Feb. .	111	5·4	36	0	147	4·1
April .	24	16·7	30	0	54	7·4
Totals	613	31·8	321	5·6	1249	20·2

TABLE III.—*Alary polymorphism in* D. muiri.

Month.	Females. Number collected.	Females. % koeliopterous.	Males. Number collected.	Males. % koeliopterous.	Males and females. Number collected	Males and females. % koeliopterous.
1955						
July .	56	57·1	44	40·9	100	50·0
Sept. .	106	95·3	91	94·5	197	95·0
Oct. .	114	95·6	101	89·1	215	92·6
Nov. .	34	91·2	12	75·0	46	87·0
Dec. .	20	40·0	10	60·0	30	46·7
1956						
Feb. .	16	75·0	6	66·6	22	72·7
April .	8	87·5	3	33·3	11	72·7
Totals	354	84·7	267	80·1	621	82·3

number of koeliopterous females of *P. saccharicida* was comparatively low during the summer months[2] but exceeded that of macropterous females during the winter months of July and September. Koeliopterous males were always uncommon but these also tended to be more numerous during the winter. The increased proportion of short-winged females during the cooler months is in accord with observations made in Hawaii (Kirkaldy, 1906) during those early years of this century when *P. saccharicida* was abundant there. Brachypterism was more prevalent in *D. muiri* and short-winged forms usually predominated in both sexes. This species became very scarce in the locality selected for sampling and some of the collections were unavoidably small.

The macropterous forms of both species seem more active than the koeliopterous forms. The former will hop at the slightest provocation, using their wings to control themselves in mid-air or to augment their leap with a short

[2] Mauritius has two distinct seasons, the summer or hot season from November to April and the winter or cool season from May to October.

flight, but the latter are much less inclined to jump and may use this method of escape only as a last resort.

III. Distribution, Abundance and Dispersion.

1. Abundance and Distribution.

An appreciation of the abundance and distribution of *P. saccharicida* and *D. muiri* in the cane-growing areas of the island was obtained by the following methods. Firstly, the abundance of egg spots in leaf mid-ribs was observed in various fields and at the same time leaf samples were taken to breed out the young nymphs and so determine the proportion of eggs laid by each species. Secondly, the abundance of egg spots in cane leaves was noted, without determining the species responsible, whenever opportunity offered. Thirdly, the abundance of nymphs and adults was judged by the ease with which they could be collected. The best criterion of leafhopper abundance was considered to be the readiness with which the active stages could be collected, for egg spots accumulate and only a proportion contain unhatched eggs. The number of eggs in the leaves also bears no direct relationship to the number of adults present, for many of the latter may be sterile owing to parasitism. Furthermore, egg parasitism has to be taken into account if the number of eggs in leaf samples is assessed by counting the emerging nymphs. The observations covered a period of nearly two years and, while their results can be expressed only in general terms, a reliable picture of leafhopper activity under different climatic, seasonal and food-plant conditions was obtained.

The most important fact which emerged was that both species of leafhoppers are seldom numerous in cane fields. The nymphs and adults were generally difficult to collect and often a thorough search would fail to reveal any. On the other hand, fields were seldom encountered where egg spots did not testify to their presence. The occasional relatively high leafhopper populations which were found were of sufficient magnitude to enable the active stages to be collected with ease, despite their concealed habits, but were neither sufficient to suppress cane growth nor to permit enough honey-dew accumulation for conspicuous growths of black fungus (*Capnodium*) on the leaves. These comparatively high populations were never extensive, occupying only a few acres.

The two species were always found together and, if one was numerous, the other was usually so also. It cannot be said that one is generally more common than the other.

As experience of collecting the active stages was obtained, it became clear that some fields were more likely to harbour numbers of the leafhoppers than others and that fields which promised to be good collecting sites could be selected by the character of the cane growth. Generally, the leafhoppers were most numerous in fields of young virgin (*i.e.* plant) cane, where the foliage had grown enough to provide adequate shelter but before the development of any appreciable length of stem. Early ratoon growths were less favoured by the leafhoppers. Otherwise, in tall cane, where the leafhoppers are very seldom abundant, more were present in tangled, recumbent growth and where the dead leaves had not been stripped prior to harvest, as is the custom in Mauritius. The observations of Urbino (1927) on *Perkinsiella vastatrix* Bredd. in the Philippines are similar; he states that virgin and ratoon cane become

susceptible to attack one to one and a half months after planting and four months after ratooning, respectively, and that mature cane is relatively free from attack.

The variety of cane also appears to influence leafhopper abundance. On those varieties with an erect habit of growth and comparatively straight leaves the leafhoppers were always scarce. On one occasion a heavy infestation of both *Perkinsiella* and *Dicranotropis* was found on young virgin growth of var. M. 134/32, which has broad, arching leaves, yet an adjoining field of var. B.3337 of the same age, with the erect and rather narrow leaves of this variety, was virtually free from infestation. Ingram *et al.* (1939) in Florida have remarked that the sugar-cane Delphacid *Saccharosydne saccharivora* Westwood is also less numerous on narrow-leaved varieties.

No distinct relationship was observed between seasonal changes and leafhopper abundance, although the impression was gained that collection of the active stages was easier during July to September (in the cool season). Either seasonal variations are of small magnitude and are masked by the general low populations and the difficulty of finding the localised " outbreaks ", or other factors, such as natural enemies, are dominant and override the effect of temperature and other seasonal changes. There was, however, a fairly distinct, but by no means pronounced, difference between the general abundance of the leafhoppers in the relatively dry, warm, low-lying districts and in the cool, wet upland areas above about 1000 feet. The leafhoppers were less numerous in the latter, where even egg spots were often hard to find.

2. Dispersion.

Dispersal of the leafhoppers may occur either by migration from plant to plant or by sustained flight. The extent to which the former occurs is difficult to judge, but in a cane field of uniform growth there would seem to be little stimulus for any considerable movement of that kind. Flight is restricted to those adult forms which possess functional hind wings, *i.e.* the macropterous forms, and the varying incidence of such forms, which are present throughout the year at least to some extent in both species, has been described above. Dispersal by flight is also governed by weather conditions, judging by the abundance of the insects at light. Over a three-year period, the author found that he could collect both species at light only on still, oppressive summer evenings. Pemberton (*in* Robinson and Martin, *in press*), in Hawaii, referring to *P. saccharicida*, observes similarly that leafhopper flights occur most frequently on quiet nights when air currents are at a minimum.

IV. Natural Enemies.

1. *Ootetrastichus pallidipes* Perkins (Eulophidae).

This species was described by Perkins (1912) from specimens collected in Java, where it attacks the eggs of undetermined species of sugar-cane leafhoppers. It has not, until now, been recorded from any other country. In Mauritius it is a parasite of *Perkinsiella saccharicida*, *Dicranotropis muiri* and *Peregrinus maidis* and seems to attack the eggs of all three with equal facility. The *Ootetrastichus* sp. earlier recorded from the eggs of *Perkinsiella* in Mauritius (Williams and Mamet, 1954) was actually *O. pallidipes*.

The life cycle of *O. pallidipes* is similar to that described for other members of the genus (Perkins, 1906*b*, 1907; Swezey, 1936). The larva develops to its last instar within the host egg, the contents of which are entirely consumed. It then breaks the chorion of the egg and burrows into the adjacent leaf tissues, where it may either pupate at once, after excavating a small pupal chamber, or it may for a while become predacious. The adult bites its way to the exterior leaving a neat round hole in the leaf epidermis.

The predacious habit during the last larval instar seems to be normal, and larvae usually increase considerably in size after leaving the host egg. The larvae may burrow as much as an inch within the mid-rib tissues of a cane leaf and they will feed not only upon healthy and parasitised leafhopper eggs but also, as was seen on two occasions, upon pupae of their own kind. *Ootetrastichus* is, perhaps, unique in being parasitic, predacious and cannibalistic during one larval instar.

The adults vary considerably in size and this may be attributed to the feeding of the larva after leaving the host egg. Parthenogenesis is normal and only one male was obtained among over a hundred adults bred from cane and maize leaves. The male obtained fits very well the description of the males ascribed to the species by Perkins (1912). It is very distinct from the female in the greatly dilated scape of the antenna and also in its pigmentation.

2. *Paranagrus optabilis* Perkins (Mymaridae).

Described in 1905 (Perkins, 1905*c*), the recorded distribution and hosts of this parasite are as follows:

Queensland: *Perkinsiella saccharicida* Kirk. (Perkins, 1905*c*).

Hawaii (introduced from Queensland): *P. saccharicida* Kirk (Swezey, 1936), *Peregrinus maidis* (Ashm.) (Zimmerman, 1948).

Samoa: *Perkinsiella vitiensis* Kirk. (Swezey, 1941).

Guam: *P. thomsoni* Muir (Swezey, 1940). The parasite is stated to be "apparently *P. optabilis*".

Java: Host unknown (Girault, 1914).

Malaya: *Sogota furcifera* Hor. (Pagden, 1934).

A very similar form, likely to be *optabilis*, is also recorded from Fiji where it attacks *P. vitiensis* Kirk. (Perkins, 1905*c*; Muir, 1906).

The parasite, which is recorded here for the first time from Mauritius, is very common and occurs generally in the eggs of both *P. saccharicida* and *D. muiri*. One specimen was also bred from a maize leaf infested with eggs of *P. maidis*, but it is clear from other attempts to recover it from maize leaves that it does not normally attack eggs of this leafhopper in Mauritius.

Accounts of the biology of *P. optabilis* are given by Perkins (1905*c*) and Swezey (1936). The biology of the insect in Mauritius seems to differ only by the greater abundance of the males. The two authors quoted state that *P. optabilis* is normally parthenogenetic and that males only appear at intervals and in small numbers. This is not so in Mauritius where males are common, although less numerous than females; of 87 adults reared at intervals from cane leaves in 1955, 33 were males.

3. *Anagrus flaveolus* Waterhouse (Mymaridae).

This species attacks the eggs of *Perkinsiella saccharicida*, *Dicranotropis*

muiri and *Peregrinus maidis* in Mauritius and this is its first record from the island.

A. flaveolus was described (Waterhouse, 1913) from specimens obtained from eggs of *P. maidis* in Trinidad. Dozier (1932) records it from the same host in Haiti and also from *Saccharosydne saccharivora* Westw. in both Haiti and Puerto Rico. Box (1953) records it from *S. saccharivora* in Cuba and Venezuela.

A closely allied form is *A. frequens* Perkins (1905*c*), which attacks eggs of undetermined Delphacidae in Queensland and which was introduced into Hawaii in 1904 against *P. saccharicida*. It became abundant on that host in Hawaii until *Paranagrus optabilis*, which was introduced shortly afterwards, displaced it. It is now a common parasite of *P. maidis* in Hawaii but is rarely seen in cane fields (Swezey, 1936). Perkins (*quoted in* Waterhouse, 1913) states that *A. frequens* attacks species of four different genera in Hawaii.

The only morphological distinction between *A. flaveolus* Waterh. and *A. frequens* Perk. lies in the distribution of the hairs on the fore wings. The clear, pale, lemon-yellow colour of *flaveolus* is also not characteristic of *frequens*, which has a distinct pattern of fuscous areas on the body. The description of *flaveolus* was, however, made from spirit-preserved specimens and possibly some of their pigmentation had been lost. Perkins (*in* Waterhouse, 1913) states that the two forms may be local races of the same species.

The arrangement of the hairs on the fore wings of the Mauritian insect agrees with the description of *flaveolus*. The pigmentation, however, agrees with that described for *frequens* except that, as was determined by direct comparison with fresh specimens of *frequens*, the fuscous areas on the body are of a much lighter shade and in some individuals are very faint. The author does not consider that there is sufficient reason to separate the Mauritian and the American insects on the basis of pigmentation differences. On the other hand, although *flaveolus* and *frequens* may actually be of less than specific rank as suggested by Perkins, the pattern of the hairs on the fore wings was found to separate the Mauritian specimens easily from those of *frequens*.

A. flaveolus is at once distinguished from *Paranagrus optabilis* by its small, almost globular, third antennal segment. It also lies, before emergence, with its head either towards or away from the cap of the host egg, and the adult always bites its way out leaving a round hole in the epidermis similar to that made by *Ootetrastichus*. *Paranagrus* is always orientated in the host egg with its head at the cap end, and the adult emerges without injuring the leaf tissues.

A. flaveolus was found in eggs of *Perkinsiella* and *Dicranotropis* only in cane in the immediate vicinity of maize infested with *Peregrinus* and it seems, as with *A. frequens* in Hawaii, to be chiefly a parasite of this latter host.

Parthenogenesis is normal and only one male was obtained among 430 adults bred from maize leaves in January and February, 1956. Waterhouse (1913) did not describe the male of *A. flaveolus*. It is, except for the pattern of hairs on the fore wing, similar to the male of *frequens* and, as in that species, has darker pigmentation than the female.

4. *Pseudogonatopoides mauritianus* Williams (Dryinidae).

This parasite was recently described by the author (Williams, 1956*b*). It attacks both *P. saccharicida* and *D. muiri* and was first collected in March,

1955. Other species of Dryinidae are known to attack *P. saccharicida* in Hawaii and Queensland. These are *Ecthrodelphax fairchildii* Perk., *Haplogonatopus vitiensis* Perk. and *Pseudogonatopus hospes* Perk. in the former (Swezey, 1936), and *Pseudogonatopus saccharetorum* Perk. in the latter (Perkins, 1906*a*).

P. mauritianus attacks only the nymphal stages of its hosts and the ectoparasitic larva becomes fully grown and kills its host when the latter is in either the third, fourth, or fifth nymphal instar. The larval sac is black and the integuments of which it is composed are finely sculptured. The position of the sac on the host is usually in the pleural region between the fifth and sixth abdominal tergites, although it has also been seen beneath a wing pad. It is not known where pupation occurs in the field. The duration of the pupal stage in the laboratory was 18 to 24 days (March to April).

The parasite is rare on *Perkinsiella* and *Dicranotropis* in the field, and only a dozen or so parasitised nymphs were collected. Its rarity may be due to the hyperparasitic *Cheiloneurus gonatopodis* Perk. (Encyrtidae), which attacks *Pseudogonatopoides* larvae and emerges from its cocoons.

5. *Elenchus templetoni* Westwood (Strepsiptera).

Elenchus templetoni Westwood (1836) was described from males collected in Mauritius by Robert Templeton in 1834. Templeton did not know the host and was therefore unable to obtain the females. The discovery, during this work, that *E. templetoni* attacks *D. muiri* is the first host record, and it is also the first time that the insect has been collected since Templeton originally found it. Strangely enough, stylopised individuals of *Dicranotropis* were first seen in the Black River district within a few miles of the type locality of *E. templetoni* as far as this can be determined from Templeton's notes (*in* Westwood, 1836). Subsequently, the parasite was found in *Dicranotropis* in several widely-separated localities and it appears to occur generally in this host. *P. saccharicida* is not a suitable host, for, as will be described later, although it is readily attacked by the triungulin larvae, development of the parasite to the extruded stage is never accomplished. Other hosts were sought on several occasions by sweeping wild grasses. Several specimens of *Delphacodes propinqua* Fieb., a cosmopolitan Delphacid, were caught with female *Elenchus* indistinguishable from those of *E. templetoni* but, unfortunately, none were obtained with male puparia from which the free-living males could have been bred.

Previous records of Strepsiptera attacking *Dicranotropis* and *Perkinsiella* are those of Muir (1906), who found *Elenchoides perkinsi* Pierce in *P. vitiensis* Kirk. in Fiji, and Pierce (1918), who records *Muirixenos dicranotropidis* Pierce and *M. perkinsiellae* Pierce (Halictophagidae) from *D. muiri* and *P. saccharicida* respectively, collected by Muir in Java.

The relationship of many species of *Elenchus*, and of similar species now placed in separate genera, is uncertain. Hassan (1939) discussed the matter to some extent and suggested that nearly all Strepsipterous parasites of Delphacidae belong to one species, *Elenchus tenuicornis* (Kirby). It is not intended to consider here the systematic position of *E. templetoni* Westw., but only to draw attention to the possibility that it may not be a distinct species. The adult male of *E. templetoni* is not described in this account for the author,

who had no specimens of other described species for comparison, found no characters to distinguish it from the male of *E. tenuicornis* as described by Hassan (1939). The other forms of *E. templetoni* are described in detail. The triungulin larva does not differ greatly from that of *E. tenuicornis* as described by Perkins (1905*a*) and Hassan (1939). The subsequent larval stages of an *Elenchus* have never been properly described. Hassan (1939) attempted to follow the larval development of *E. tenuicornis*, but he was handicapped by shortage of material and his descriptions of the successive developmental forms are confused.

(*a*) Descriptions of the various stages.

The triungulin larva was described from specimens obtained from a parturient female and mounted in de Faure's medium.

The subsequent larval forms were described from fresh and alcohol-preserved specimens examined in alcohol with a binocular microscope giving magnification of up to × 48. A large series of these intermediate forms was obtained by dissection of field-collected *Dicranotropis*. The author was aided by an opportune discovery of a fairly large leafhopper population, sited near a main road, where the parasite was very common. Fresh specimens were thus conveniently at hand and their abundance aided greatly the grouping of the successive developmental forms. Nevertheless, the number of instars could not be determined with certainty, for sclerotisation is completely absent except in the last instar, which has sclerotised mouth parts. The enumeration of the instars is therefore tentative and is based chiefly upon the number of distinct forms which are evident during growth. Even this method of separating the various stages was possible only because specimens were plentiful, for there is some variation of form within each instar depending upon the degree of distention of the integument.

(i) *The First Larval Instar, or Triungulin* (fig. 3*a*).

The length of the body, excluding the posterior setae, is about 0·15 mm. The integument is moderately sclerotised except for the abdominal sternites, which are very lightly sclerotised.

The head fits closely with the prothorax, and the eyes have several lenses with an underlying mass of black pigment. The mouth parts are exceedingly minute and situated at the extremity of the head (they could not be resolved and are not shown in the figure). The antennae are prominent, unsegmented, and terminate in a long seta ; they are placed ventrally on the head below the mouth parts.

The thoracic segments are large with the prothorax longer than the mesothorax and the latter longer than the metathorax. The three pairs of legs are similar ; the large coxae meet, or nearly meet, at the mid-line and each bears an inner seta ; the femurs are broad and the tibiae are slender ; the tarsi are spine-like and each terminates in two small spines, one of which is longer than the other.

The abdomen has ten segments. The first eight are similar, with the tergites recurved ventrally and each recurved part bearing a seta ; their sternites are much narrower than the width of the body, very slightly sclerotised, and with a

pair of fine setae at the mid-line. The ninth and tenth segments are larger than the preceding segments. The posterior edge of the ninth tergite projects backwards laterally and the sternite has two pairs of slender setae and also a pair of elongate projections, each of which bears a large terminal spine. The tenth segment is large and bears two very stout spines about 0·1 mm. in length.

(ii) *The Subsequent Larval Instars.*

Hypermetamorphosis follows the first larval stage and the subsequent larval instars have the degenerate structure which typifies many internal parasites. All the stages are creamy-white in colour and no mouth is discernible.

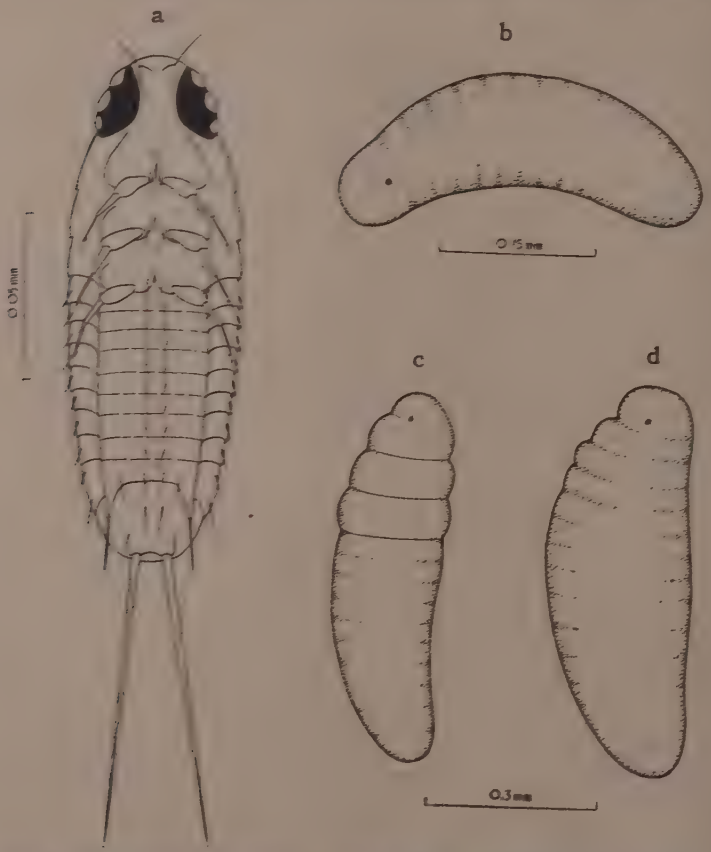

FIG. 3.—*Elenchus templetoni* Westw. (*a*) Triungulin. (*b*) Second larval instar. (*c*) Third larval instar, male. (*d*) Third larval instar, female.

The second larval instar (fig. 3*b*).—The length of the specimens examined varied from 0·25–0·4 mm. The body is indistinctly segmented and tapers towards each end; it is curved, with the ventral side convex, in the smaller

individuals and more or less fusiform in the larger ones. The head is slightly flattened dorsoventrally and has dark eye-spots.

The third larval instar.—The sexes are distinguishable in this instar. The male larva (fig. 3*c*) is more slender than the female and has comparatively large thoracic segments which are well defined except at the dorsal junction with the head. The female larva (fig. 3*d*) has a ventral indentation between

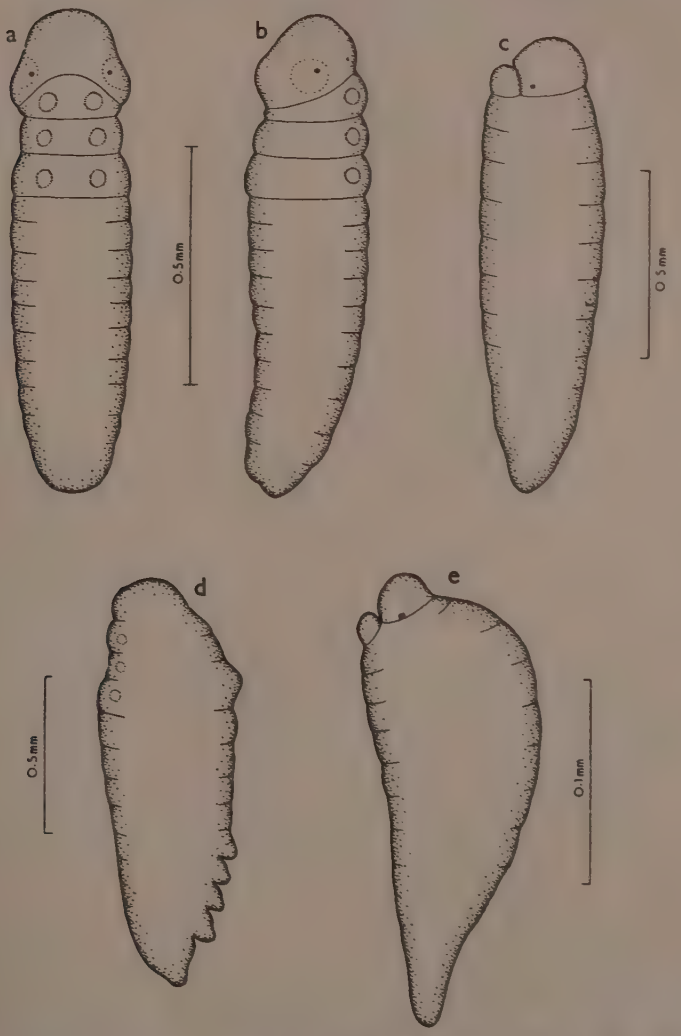

FIG. 4.—*Elenchus templetoni* Westw. (*a*)–(*b*) Fourth larval instar, male, ventral and lateral views, respectively. (*c*) Fourth larval instar, female. (*d*) Fifth larval instar, male. (*e*) Fifth larval instar, female.

the head and the thorax and the three thoracic segments bulge ventrally. In both sexes the body is slightly curved, about 0·5–0·7 mm. in length, and the eye-spots are distinct as in the previous instar.

The fourth larval instar.—The male (figs. 4*a*, *b*) is between 0·65–1·0 mm. in length. Its head is bulbous and broader than the thorax. The thoracic segments are large and each has leg rudiments in the form of conspicuous projections. The abdomen is slender.

The female is shown in figure 4*c*. A bulbous structure is present ventral to the head and will be termed the " thoracic lobe ", although its derivation is obscure.

The form of the female of this instar is essentially the same as that of the fully-grown female larva and subsequent changes appear to consist merely of increase in size and greater approximation to the pear-shaped form of the latter. As a result, the number of female instars which follow is uncertain. However, the size range among female larvae of this form and the enclosure of a few of those examined in a complete, loose, integument, shows that at least one instar intervenes between the fourth and final female larval instars.

The fifth larval instar.—The male larva (fig. 4*d*) is 1·0–1·5 mm. in length. Its thoracic segments are large and ill defined. Leg rudiments are small and papilla-like, but in some specimens they could not be seen at all. Four dorsal, median, prominences occur on the abdomen.

The form of a female larva intermediate between the fourth and final instar, and which for convenience is termed the fifth instar, is shown in figure 4*e*.

The sixth (final) larval instar.—Extrusion through the host integument occurs during this stage and the larvae of both sexes possess mouth parts which become heavily sclerotised. The structure of the mouth parts (fig. 5*d*) is similar in the two sexes. The mandibles are 0·03 mm. wide and possess two small teeth at the apex.

The male larva (fig. 5*a*) is 1·25 mm. long immediately after moulting and increases to about 2·0 mm. before extrusion. The head and thorax are fused into a blunt cone-like structure or cephalothorax. A pair of spiracles is present on the cephalothorax and rudiments of compound eyes appear later during the instar. The dorsal prominences on the abdomen are large and the penultimate segment has two lateroventral, bluntly pointed, prominences. These prominences are fully extended (or distended) only immediately before extrusion.

The female larva (fig. 5*b*) varies between 2·5–3·5 mm. in length. A pair of spiracles is present, one in each of the angles formed by the head and the thoracic lobe. The term cephalothorax is used to designate the head, thoracic lobe and spiracles. The pear-shaped abdomen has median, dorsal prominences which vary in number and shape with different individuals.

(iii) *The Puparium* (fig. 5*c*).

After extrusion of the anterior part of the cephalothorax from the body of the host, the integument of the last instar male larva becomes sclerotised, except posteriorly, to form a puparium. The extruded part of the puparium is heavily sclerotised and is virtually hemispherical. A cephalic cap, which is pushed off completely during emergence of the adult male, is clearly demarcated by a line of fracture. The mouth parts of the larva, which are incorporated in

the puparium, remain moderately discernible on the cephalic cap. The spiracles are situated on the extruded part of the cephalothorax below the line of fracture. The pupa is not retracted from the extruded part of the puparium, although it by no means fills the puparium posteriorly. Consequently, the posterior of the puparium, which is not sclerotised, frequently collapses. The length of puparia varies from 1·7–2·25 mm.

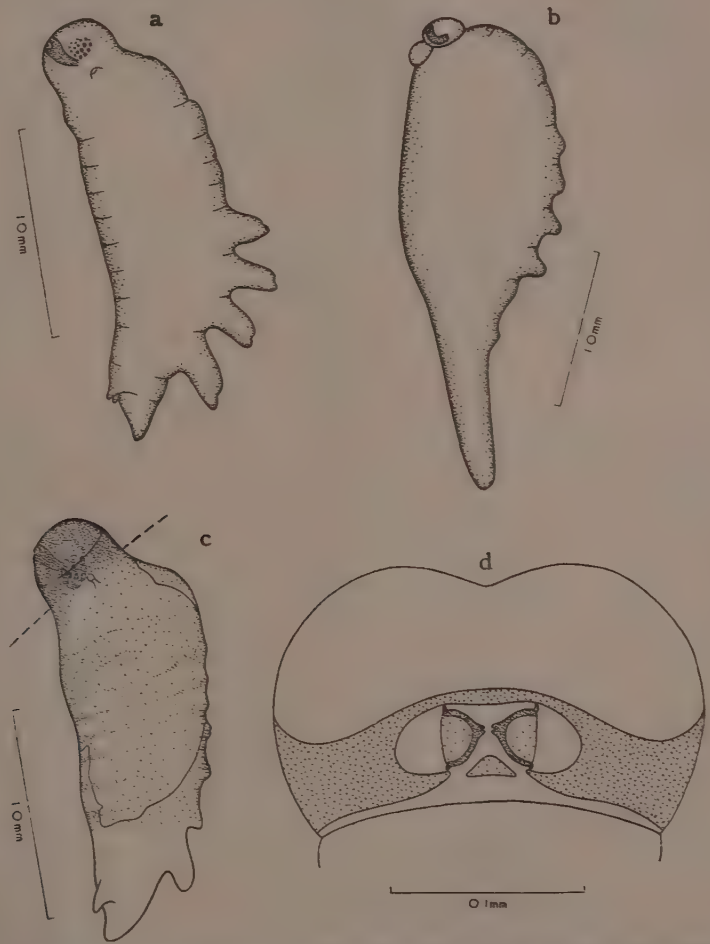

FIG. 5.—*Elenchus templetoni* Westw. (*a*) Sixth (final) larval instar, male, before extrusion. (*b*) Sixth (final) larval instar, female, before extrusion. (*c*) Male puparium (the dotted line indicates the host integument). (*d*) Mouth parts of the sixth instar female larva.

(iv) *The Pseudopuparium and the Adult Female.*

The female has no pupal stage and the last instar larva transforms to the

adult shortly after extrusion of the cephalothorax. The larval integument is not cast off and adheres closely to that of the adult, except ventrally on the abdomen where it becomes detached to form the brood canal, and over the head and around the spiracles where it is inseparable from, and presumably fused with, the adult integument. Transformation to the adult form is accompanied by sclerotisation of part of the larval integument. With specimens which have been preserved in alcohol, the persistent larval integument often separates from that of the female, except at the head and spiracles.

The external characters customarily ascribed to adult female Strepsiptera are actually those of the sclerotised portion of the persistent last larval integument. Even though the persistent larval integument is an integral part of the adult female, it seems well to avoid this practice of referring to its characters as if they were primarily characters of the adult female. Descriptive anomalies, such as references to the mouth parts of the adult (which are non-existent) and to the genital opening being between its head and thorax, are avoided if the external characters are attributed to the structure to which they belong, *i.e.* to the persistent last larval integument. The author proposes to apply the term " pseudopuparium " to this persistent integument. A special term seems warranted and " pseudopuparium " is apt, for, while the structure is clearly homologous with the male puparium, the form it envelops and protects is the imago, with which it is partially fused.

The sclerotised part of the pseudopuparium is shown in figures 6*a* and 6*b*. The form of the extruded portion follows that of the cephalothorax of the last instar larva and consists of two lobes. The larger of the lobes is derived from the integument of the larval head and now invests, and is inseparable from, the head of the adult female. The smaller, ventral, lobe—the " thoracic lobe " of the larva—is a hollow structure unoccupied by the body of the female. A spiracle is present in both angles formed by the head and the empty thoracic lobe. These extruded structures constitute the adult female cephalothorax of authors. The width of the pseudopuparium over the head is about 0·28 mm. and that of its thoracic lobe about 0·20 mm. Their overall length is about 0·33 mm. The dimensions are approximations, for the shape of the head and thoracic lobes of the pseudopuparium depend to some extent upon the pressures exerted by the host integument on the extruded larva, that is, upon the constriction around the base of the larval cephalothorax where it tends to be pinched off by the host integument. As extrusion occurs not only through the membranous pleural region of the host abdomen but also between the tergites and sternites, the constricting action of the host integument varies accordingly. The mandibles of the larva, and often its associated structures as well, remain discernible on the pseudopuparium, the former appearing as U-shaped thickenings. Two groups of pores are present above the remains of the mouth parts, as shown in figure 6*b*. The thoracic lobe is intact on the young adult but part of it is lightly sclerotised and is broken away, presumably by the male during fecundation, to form the genital opening. The remaining, more heavily thickened, part of the lobe forms a shallow hood around the genital opening and is crescentic in form when viewed from above. Within the body of the host, the sclerotisation of the pseudopuparium extends over the base of the abdomen of the female, where it is wrinkled owing to the constriction at the point where it issues from the host. A sclerotised strip also extends ventrally

over the abdomen of the female, from which it is separated to form the brood canal. Segmentation is apparent on this sclerotised strip, while small oval areas of a lighter shade indicate the position of the genital pores on the female within. The brood canal opens to the exterior through the genital opening on the thoracic lobe.

The female itself is almost a featureless bag filled with eggs. It is intimately fused with the pseudopuparium at the head and at the spiracles and more lightly attached to it around the margin of the brood canal. The thorax is in evidence only by the presence of spiracles. The abdomen is pear-shaped and in young females (fig. 6*a*) has dorsal prominences of irregular shape and number which disappear as the body becomes distended with developing eggs. There are three genital pores opening into the brood canal.

(*b*) Biology.

In this and the following sections concerning *E. templetoni*, " the host " refers to *D. muiri*, unless stated otherwise, and " stylopised " is used to denote parasitism by any stage of *Elenchus*, i.e. not only to denote hosts with extruded *Elenchus*. " Triungulin " is used for the first instar larva and " larva ", when unqualified, means a larval stage subsequent to the triungulin.

(i) *The Life Cycle.*

The eggs, which are free in the body of the female, develop simultaneously and the body is eventually filled with a tightly-packed mass of triungulins ready for eclosion and escape to the exterior *via* the genital pores, the brood canal and the genital opening. The pigmented eyes and the sclerotised integument of the triungulins impart a dark colour which is visible through the integument of the host and by means of which the imminence of parturition can often be determined. Fecundity is of the usual high order found in the Strepsiptera ; the developing eggs in three females were counted and they totalled about 2240, 1130 and 1790, respectively. In another female where parturition had begun, 1380 triungulins and eggs ready for eclosion were found. Although the eggs mature simultaneously, eclosion begins with those nearest the genital pores and the body of a female never contains a mass of free triungulins. Very few triungulins fail to leave the body of the female which, after parturition, is a shapeless, flaccid, sac loosely filled with opaque fatty tissue. The period required for emergence of the whole brood was not assessed.

The triungulins encounter their hosts upon the cane foliage and presumably use their minute mouth parts to effect entry through the host integument. They have been found in all nymphal instars and in adults of field-collected *Dicranotropis*. In very small nymphs, the triungulins are usually visible through the integument of the abdomen when examined under a binocular using transmitted light. The occurrence of the triungulins in first instar nymphs is particularly interesting, as Kirkpatrick (1937) found that *Corioxenos antestiae* Blair, a parasite of *Antestia* spp., would enter nymphal hosts only during an ecdysis and, accordingly, first instar nymphs were free from attack.

There are probably five larval instars subsequent to the triungulin. Feeding is apparently by abstraction of nutrients from the blood of the host, for no mouth is visible and the mouth parts, which disappear after the triungulin

stage to reappear only in the last instar larva, are obviously not used for feeding. The bodies of the larval instars subsequent to the triungulin are creamy-white and without muscular convolutions. They were never seen to move even when dissected out in Ringer's solution but some power of movement must exist at least during the final larval instar when the cephalothorax is extruded through the host integument. The final larval instar possesses a pair of well developed mandibles with a form and an articulation which permit only a pinching action. These mandibles must be the means whereby the host integument is punctured to allow extrusion of the cephalothorax. A series of prominences on the body of the last instar larva are fully inflated prior to extrusion and it seems that they assist or enable the body movements necessary to effect extrusion.

After extrusion of the larval cephalothorax, female larvae moult to the adult stage within the persistent larval integument which becomes the pseudopuparium. Male larvae transform into pupae after extrusion and the last larval skin hardens to form a puparium. The adult, free-living, male emerges by pushing off the cap of the puparium.

(ii) *Extrusion.*

Extrusion of female larvae seems to occur only when the host is adult, but the cephalothorax of male larvae is extruded also from fifth, and less frequently from fourth, instar nymphs. This agrees with the observations of Hassan (1939) on *E. tenuicornis*. Perkins (1905*a*), referring to the same species, stated that the extruded stages of both sexes are borne by nymphal and adult hosts.

In adult hosts, extrusion of both sexes occurs normally through the membranous pleural integument of abdominal segments five to eight between the tergites and the pleurites (laterotergites of Kramer, 1950). It occurs less frequently between the lateral ends of the tergites or between the pleurites and the sternites while, very occasionally, it also occurs between the sternites. Extrusion of male larvae from nymphal hosts seems to occur with facility from all parts of the abdomen which, of course, is comparatively lightly sclerotised.

Extruded puparia tend to lie at an angle to the host integument, as shown in figure 5*c*. The extruded females always have their ventral surface more or less apposed to the host integument (fig. 6*a*), and they lie with the head towards the posterior of the host and the tail tapering forward into the base of the host abdomen and often into the thorax. Crowding within the host due to superparasitism may affect both the orientation of the female and the point of extrusion of both sexes. For example, in one host with three extruded puparia blocking the central part of the abdomen, a female, extruded behind the puparia, lay with its head directed forwards and its body bent across the terminal curve of the abdomen. When extrusion of either sex occurs between the abdominal tergites or sternites, rather than in the membranous pleural region, it is almost invariably due to crowding within the host.

The number of extruded forms found in stylopised hosts is variable and the maximum number which a host can bear at any time seems limited only by the capacity of its abdomen. Details are given in Table IV of the number of extruded parasites in 200 field-collected hosts which contained these stages; 68·5 per cent. had one extruded parasite and the remainder two, three or four. The greatest number of extruded parasites seen in a host was actually five, but

TABLE IV.—*The number and sex of extruded* Elenchus *in* 100 *male and* 100 *female field-collected* D. muiri.

Number and sex of extruded parasites.	One parasite.		Two parasites.			Three parasites.				Four parasites.			Total number of hosts.	Total number of parasites.		
			1 ♀ +			1 ♀ +	1 ♂ +			2 ♀ +	1 ♀ +	1 ♂ +				♀ +
	1 ♀.	1 ♂.	2 ♀.	1 ♂.	2 ♂.	3 ♀.	2 ♂.	2 ♀.	3 ♂.	2 ♂.	3 ♂.	3 ♀.		♀.	♂.	♂.
Hosts .	36	31	13	8	5	.	1	4	.	1	1	.	100	82	60	142
	67		26			5				2						
Hosts .	40	30	8	9	4	1	1	2	1	1	1	2	100	82	61	143
	70		21			5				4						
Total hosts	137		47			10				6			200	164	121	285

no host has been seen with more than four extruded females. Nymphs rarely bear more than one puparium and none were seen with more than two. The sex of a host does not affect the number of extruded parasites it may bear (Table IV) for, although the abdomen of a healthy male is smaller than that of a healthy female, the integument of both allows considerable distention.

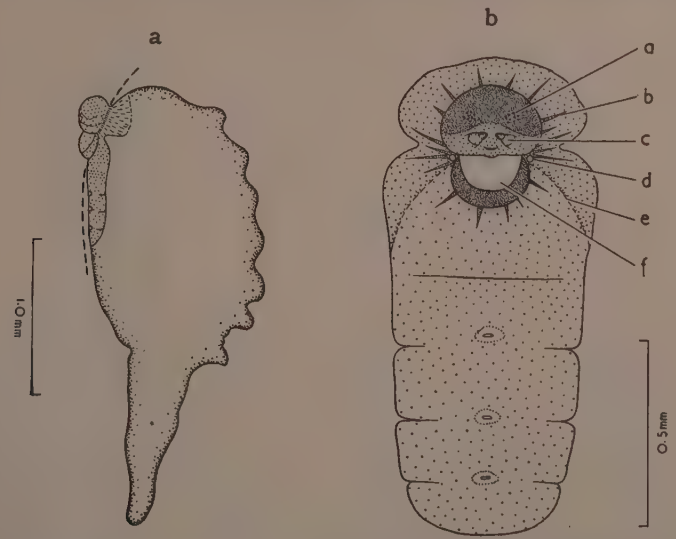

FIG. 6.—*Elenchus templetoni* Westw. (*a*) Young adult female and pseudopuparium (the constricted terminal part of the abdomen lay in the thorax of the host; the dotted line indicates the host integument). (*b*) Details of the sclerotised part of the pseudopuparium. *a*, Pores. *b*, Wrinkles of the integument. *c*, Remains of the last larval mouth parts. *d*, Spiracle. *e*, Forward limit of brood canal. *f*, Genital opening.

Unextruded puparia and adult females are sometimes found in the bodies of adult hosts. Of a dissection of 176 adult hosts, nine contained either an un-

extruded puparium or an unextruded female. Four of these nine hosts had no extruded parasites, so failure to become extruded could not be attributed to lack of space due to superparasitism. The sclerotisation of the unextruded puparia and of the pseudopuparia of the unextruded females was normal.

(*c*) The effects of stylopisation upon *Dicranotropis*.

(i) *External Effects.*

Distention and distortion of the abdomen.—This varies in degree according to the number of advanced parasites in the host. Adult females and well-developed larvae tend to distend rather than distort the host's abdomen, while the

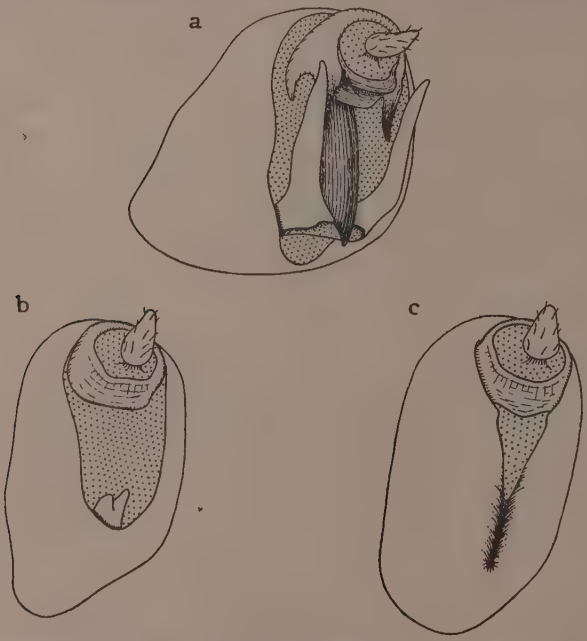

Fig. 7.—*Dicranotropis muiri* Kirk. (*a*) Male genitalia. (*b*)–(*c*) Reduced male genitalia following stylopisation.

opposite is true of puparia, which are more or less rigid structures with a comparatively large cephalothorax. The abdomen of the host consequently tends to bulge where puparia are extruded and the sclerites are more liable to be displaced. When extruded puparia are present in nymphs, the abdomen, owing to its comparatively small size, virtually loses its form and assumes that of the puparium.

In female hosts, distention tends to make the abdomen globular while the abdomen of male hosts, owing to the different form of the segments consequent upon the absence of an ovipositor, tends to elongate and become sausage-shaped, bending down at its extremity.

Splitting of the integument.—The thin pleural integument of the abdomen sometimes splits considerably near, or at, the point of extrusion of a parasite.

The wound heals (at least it does so frequently, but perhaps death sometimes results in the field) and a black patch, or a black margin, remains to define its limits.

Alteration of sexual characters.—There are no secondary sexual characters apparent in *D. muiri*, except for the somewhat different shape and smaller size of the abdomen in the male, and stylopisation has no discernible effect upon general body structure or pigmentation of either sex.

The primary sexual characters, however, are affected in a proportion of stylopised hosts of both sexes. The aberrations in male hosts are the absence or reduction of the aedeagus and parameres, the altered proportions of the pygofer and of the size and shape of its cavity, and the simplified ring-like form of the anal segment. The aedeagus of affected hosts is frequently absent but the parameres of most are present as reduced, shapeless, structures which are often fused at their bases. Figure 7 illustrates these aberrations. No stylopised male host was seen with slight aberrations of the genitalia; the changes were either of the drastic nature described or they were absent.

TABLE V.—*The length of the ovipositor of healthy and stylopised* D. muiri.

Ovipositor length in units (1 mm. = 28 units).	Number of healthy *D. muiri*.	Number of *D. muiri* with extruded *Elenchus*.
25	.	1
26	.	1
27	.	1
28	.	2
29	.	2
30	.	6
31	.	3
32	.	3
33	1	1
34	2	1
35	9	5
36	23	10
37	10	11
38	4	2
39	1	1
Number of *D. muiri* examined	50	50
Mean length of ovipositor	36·10	33·70
Standard deviation	0·348	3·637
Difference between means	2·4	
Standard error of difference	0·516	

In stylopised female hosts, the length of the ovipositor and of its sheath may be reduced. Table V gives the lengths of the ovipositors of 50 healthy hosts and hosts with extruded *Elenchus*, respectively, and the two lots were random samples of such hosts. The ovipositors were measured after removal of their sheaths and the measurements are given in units of a micrometer eyepiece. It should be noted that "healthy" hosts were dissected to ensure that they contained no internal parasites of any kind apart from triungulins, which were ignored, for their detection necessitates very careful dissection and their

presence could not have affected development of the genitalia. The difference between the mean length of the ovipositor of healthy and stylopised hosts is highly significant and the frequency table shows that an ovipositor length of 32 units or less may be considered abnormal.

TABLE VI.—*The frequency of aberrant genitalia in a field-collected sample of* D. muiri.

(a) *Females.*

Conditon of host.	Healthy.	Stylopised. With extruded *Elenchus*.	Stylopised. With internal *Elenchus* only.	Stylopised. Total.	Parasitised by *Dorilas*.	Totals.
Number of hosts . . .	50	23	26	49	15	114
Number of hosts with aberrant genitalia	0	10	4	14	4	18
% of hosts with aberrant genitalia	0	43·5	15·4	28·8	26·6	15·8

(b) *Males.*

Condition of host.	Healthy.	Stylopised. With extruded *Elenchus*.	Stylopised. With internal *Elenchus* only.	Stylopised. Total.	Parasitised by *Dorilas*.	Totals.
Number of hosts . . .	35	17	29	46	30	111
Number of hosts with aberrant genitalia	0	10	13	23	4	27
% of hosts with aberrant genitalia	0	58·8	44·8	50·0	13·3	24·3

The frequency of aberrant genitalia in *Dicranotropis* in the field is indicated by the data in Tables VI*a* and VI*b*. The male and female *Dicranotropis* were all collected in the same field during the same week of October, 1955. The genitalia of the females were considered to be aberrant if the ovipositor was less than 33 units in length, and " healthy " hosts again refers to those without parasites or with only triungulins in their bodies. It is seen from the tables that parasitism by *Dorilas mauritianus* Hardy (Pipunculidae), a parasite which is considered later, also causes aberrations of the genitalia. Multiparasitism,

with *Dorilas* larvae and stages of *Elenchus* subsequent to the triungulin, occurs only exceptionally and there was therefore no difficulty in attributing the abnormality of a host's genitalia to the correct parasite.

It seems probable that the state of the genitalia in stylopised hosts (and also in those parasitised by *Dorilas*) depends primarily upon the stage of the host when attacked, those attacked early in their development having aberrant genitalia. It may also depend to a certain extent upon the degree of superparasitism, although no correlation between this factor and aberrance of the genitalia was evident. Superparasitism does not occur with *Dorilas*, so that the factor cannot be involved when this parasite is the cause of aberration. Hassan (1939), who studied stylopisation of several species of Delphacidae in England, noted that reduced genitalia occurred in species which overwintered in the nymphal stage but not in those which overwintered as eggs and had a comparatively short period of nymphal development. In Mauritius, the seasonal changes are not pronounced and *Dicranotropis* breeds throughout the year without distinct generations.

(ii) *Effect upon the Internal Organs.*

Only the triungulin and the final larval instar possess mouth parts and in both their function is presumably only to perforate the host integument to effect entry and extrusion, respectively. A mouth is not evident in any stage, although histological examination is necessary to ascertain its absence. It seems probable, therefore, that feeding is entirely by diffusion or absorption of nutrients from the blood of the host. There is certainly no possibility of mechanical injury to the internal organs of the host by any stage except the triungulin and last larval instar. No such injury was, in fact, apparent during dissections of *Dicranotropis* but it is difficult to be quite sure, by such means, that none occurs.

Only the sex organs are physically altered by stylopisation and the alimentary canal, although displaced by well-grown larvae and extruded forms, shows no abnormality. The effect upon the sex organs is usually considerable in both male and female hosts except when they contain only small *Elenchus* larvae. The sex organs may then appear normal with, in female hosts, apparently mature eggs. In hosts with advanced larvae or extruded forms, the sex organs are almost invariably either reduced or it is not possible, by dissection, to find any trace of them. All parts of the reproductive system are affected in male hosts and the whole is usually of diminutive size. In female hosts, it is frequently only the ovaries which are reduced and devoid of mature eggs. There is, generally, an obvious correlation between the size of the parasites and the degree to which the sex organs are reduced and it is to be concluded that atrophy, in the true sense of the word, coincides with the development of *Elenchus* in adult hosts. In addition, the development of the sex organs may be abortive if a well-developed *Elenchus* larva is present in a host before it moults to the adult stage. For example, a freshly moulted adult male host with aberrant genitalia was found, on dissection, to contain an advanced female larva and, while the accessory glands were prominent, other organs could not be traced.

(iii) *Effects upon the Biology.*

Reproduction.—It will be appreciated from the preceding sections that the sexual functions of *Dicranotropis* are seriously impaired by stylopisation. In stylopised female hosts, the sex organs are normal and with mature eggs only in some individuals which contain small or fairly small larvae. It was determined in the laboratory that such hosts will lay fertile eggs. The fertility of stylopised male hosts with normal genitalia was not determined, but it seems probable that those with small *Elenchus* larvae are, like female hosts in a similar state, fertile for a while. The diminutive organs of most stylopised male hosts including those with normal genitalia, can hardly be functional.

Premature death. Male *Elenchus* larvae may become extruded during the fourth or fifth nymphal host instars but the female larvae are extruded only in adult hosts. Nymphs with extruded puparia never develop further and those kept in the laboratory always died within a matter of hours after emergence of the adult male parasite. Observations upon the duration of adult life following emergence of male *Elenchus* from the puparia and following parturition of female parasites were not made. Many adult hosts were, however, collected with empty puparia and a smaller number with females which had completed parturition. It is, at least, clear that death of the adult host does not always follow rapidly after emergence of the male *Elenchus*. Moreover, some empty puparia in live hosts contained a growth of fungus which required a certain time to develop.

(*d*) The incidence of stylopised *Dicranotropis* in the field.

The stylopisation of *Dicranotropis* adults, collected from three fields, each in a different locality, is shown in Table VII. In each of the fields *Dicranotropis*, and also *Perkinsiella*, were comparatively abundant and reasonable numbers to assess stylopisation were obtainable. It has already been mentioned that the leafhoppers are not generally numerous and it is normally difficult to collect them in quantity. The data in Table VII are therefore not representative of conditions generally but pertain to comparatively high, localised, populations. This does not detract from their value as an indication of the significance of *Elenchus* as an agent of natural control.

Some of the *Dicranotropis* were examined only for the presence or absence of extruded *Elenchus*. Others were dissected to find the internal parasites also, but the presence or absence of triungulins was not recorded owing to the meticulous dissections which this would have entailed.

The percentage stylopisation is seen from the table to have varied considerably among the several sample collections made in two of the fields (at Palmyre and Flacq), even though the time interval between the collections was small and the collecting technique was not varied. It is for this reason that the results of each collection are given separately, so that sampling errors may be appreciated. It is, however, clear that *Elenchus* was an abundant parasite of *Dicranotropis* in these fields.

The number of male and female hosts with extruded *Elenchus* is given separately. More male hosts than female hosts had extruded parasites but it is doubtful if the difference is of any significance.

It should be noted that the other parasitic species found in adult *Dicranotropis*, namely *Dorilas mauritianus*, does not normally co-exist with *Elenchus*

TABLE VII.—*The incidence of stylopised adult* D. muiri *in the field.*

Locality.	Date.	Male hosts. Number collected.	Male hosts. Number with extruded *Elenchus*.	Male hosts. % with extruded *Elenchus*.	Female hosts. Number collected.	Female hosts. Number with extruded *Elenchus*.	Female hosts. % with extruded *Elenchus*.	Total hosts. Number collected.	Total hosts. Number with extruded *Elenchus*.	Total hosts. % with extruded *Elenchus*.	Number with internal *Elenchus** only.	% with internal *Elenchus** only.	Total stylopised.	% stylopised.
Palmyre	15.iii.55	22	10	45·5	28	6	21·4	50	16	32·0	.	.	.	.
,,	16.iii.55	25	1	4·0	41	2	4·9	66	3	4·5	.	.	.	.
,,	21.iii.55	23	7	30·4	49	4	8·2	72	11	15·3	.	.	.	.
Constance	27.vii.55	44	26	59·1	56	20	35·7	100	46	46·0	10	10·0	56	56·0
Flacq	16.ix.55	56	27	48·2	67	30	44·8	123	57	46·3	16	13·0	73	59·3
,,	22.ix.55	18	2	11·1	13	3	23·1	31	5	16·1	.	.	.	.
,,	26.ix.55	17	6	35·3	26	8	30·8	43	14	32·6	.	.	.	.
,,	4.x.55	69	11	15·9	75	16	21·3	144	27	18·8	36	25·0	63	43·8
,,	7.x.55	42	6	14·3	39	7	17·9	81	13	16·0	19	23·5	32	39·5
,,	4.xi.55	12	5	41·7	34	6	17·6	46	11	23·9	10	21·7	21	45·7
Totals		328	101	30·8	428	102	23·8	756	203	26·9				

* Comprising stages subsequent to the triungulin larva.

in the same host. The data in Table VII are thus not complicated by multi-parasitism and record the effective stylopisation within the samples collected. Parasitism by *Dorilas* in the same collections is an additional parasitic factor which is considered separately below.

(*e*) Stylopisation of *Perkinsiella saccharicida*.

A total of 847 adults of *Perkinsiella* and 129 advanced nymphs, collected in cane fields infested also with *Dicranotropis*, were either examined individually or dissected and in no single one was there an extruded *Elenchus*. Many others, amounting to several hundreds, were handled in the course of this study but without an extruded *Elenchus* being seen. On the other hand, dissections of adults and nymphs always revealed that a high percentage contained triungulins and subsequent larval forms (Table VIII). Nearly all

TABLE VIII.—*Stylopisation of* P. saccharicida.

Locality.	Date.	Number collected. 4th and 5th nymphs.	Number collected. Adults.	Number with internal* *Elenchus*.	% with internal* *Elenchus*.	Number with extruded *Elenchus*.
Constance .	22.vii.55	.	160	98	61·2	0
,, .	27.vii.55	.	200	.	.	0
,, .	,,	12	.	5	41·7	0
Flacq .	8.viii.55	.	100	.	.	0
,, .	,,	117	.	63	53·8	0
,, .	11.viii.55	.	50	.	.	0
,, .	16.ix.55	.	50	38	76·0	0
,, .	14.x.55	.	50	36	72·0	0
,, .	,,	.	137	.	.	0
,, .	14.xi.55	.	100	70	70·0	0

* Comprising stages subsequent to the triungulin larva.

the larvae were small and the great majority were obviously dead, being shrunk and blackened or having a mass of black matter in the body. Some were also partly covered with a whitish matter, probably phagocytic. Some of the triungulins also were black and clearly dead. Advanced larvae, unextruded puparia and unextruded adult females were rarely found (the two latter forms in only four adult *Perkinsiella* out of 360 dissected) and most were stunted. The number of larvae (excluding triungulins) present in stylopised individuals varied from one to as many as fifteen ; typically, all would be in one of the early instars, two or three would be apparently alive and the others would be black, shrivelled, and often clustered in the terminal part of the host's abdomen.

It is evident that triungulins readily attack *Perkinsiella* but they either die or, more commonly, the larvae to which they give rise die at an early stage of development. Survival to the pupal or adult female stages is rare and extrusion is never effected. *Perkinsiella* is thus an unsuitable host for *Elenchus* and it is unsuitable because of some physiological property which inhibits larval development of the parasite.

The high incidence of stylopisation shown in Table VIII and the numbers of larvae within individuals do not indicate that the triungulins have any

aversion to *Perkinsiella*. On the contrary, it is a curious fact that many *Perkinsiella* contain more *Elenchus* larvae than are ever found in *Dicranotropis*. The presence of more than ten dead larvae, which may be accompanied by two or three which seem alive, is not uncommon in *Perkinsiella* but similar numbers were never found in *Dicranotropis*. Since dead larvae were not found in the latter and since *Perkinsiella* does not often contain more than two or three apparently live larvae at one time, a possible explanation is that triungulins are able to appreciate the presence of several living parasites in a host and may refrain from attacking such hosts.

The stylopisation of *P. saccharicida* by *E. templetoni* is a most interesting example of a parasitic insect readily attacking an unsuitable host in the field.

The development and reproduction of *Perkinsiella* is apparently quite unaffected by stylopisation. It was ascertained in the laboratory that nymphs containing *Elenchus* larvae develop to the adult stage and that adult females, similarly stylopised, lay fertile eggs. Furthermore, the sex organs of the adults always appeared normal, comparable in all respects with those of unattacked individuals. The normality of stylopised *Perkinsiella* may be accounted for by the premature death of the *Elenchus* larvae before they are large enough seriously to drain the host's blood of nutrients. The state of the sex organs of the four *Perkinsiella* adults which contained unextruded puparia and adult female *Elenchus* was unfortunately not recorded but since this condition is rare, it cannot, in any case, be of practical importance.

It is of interest to recall the attempts made to establish Elenchid Strepsiptera on *P. saccharicida* in Hawaii, as described by Muir (1906). In 1903, Koebele introduced an American *Elenchus* which failed to establish itself upon *P. saccharicida* although an *Elenchus* (stated to be *E. tenuicornis*) found subsequently to attack an endemic leafhopper is considered by Muir to be the insect introduced by Koebele. In 1906, Muir attempted to establish *Elenchoides perkinsi* Pierce, which attacks *P. vitiensis* Kirk. in Fiji. He found that *P. saccharicida* was immune from its attacks; when confined with *P. vitiensis* upon which *Elenchoides* was breeding, it never developed the parasites. The identity of the Strepsiptera concerned is uncertain. The Fijian parasite, which Muir considered to be *E. tenuicornis*, was renamed and the genus *Elenchoides* erected for it by Pierce (1909) on the strength of Muir's figures—which did not include the adult male and some of which, on Muir's own testimony, were of doubtful accuracy. What does emerge from Muir's paper (1906) is that Strepsiptera closely related, almost certainly congeneric and possibly conspecific, to *E. templetoni* did not find *P. saccharicida* in Hawaii to be a suitable host.

6. *Dorilas mauritianus* Hardy (Pipunculidae).

Both *P. saccharicida* and *D. muiri* are attacked by this parasite which was found for the first time in July, 1955, and described as a species new to science by Hardy (1956). Parasitism of *D. muiri* by Pipunculid flies has not been recorded elsewhere, but three species of *Pipunculus* are recorded from *P. saccharicida* in Hawaii (Swezey, 1936); these are *P. juvator* Perk., *P. teryii* Perk. and *P. hawaiiensis* Perk., and they are stated to be native species which normally attack native leafhoppers.

(*a*) Descriptions of the various stages.

(i) *The First Larval Instar.*

The young larva is somewhat less than 1·0 mm. long and tapers at both ends (fig. 8*a*). It eventually nearly doubles this length and becomes stout, almost globular. There are 11 segments, including the head segment, and each bears a ventral band of minute spines. A large, bilobed, vesicle is present at the posterior of the body. Spiracles are absent but the tracheal system becomes evident later during the instar.

The buccopharyngeal armature (figs. 8*b*, *c*) is well developed with distinct sclerites. The basal piece has slender dorsal and ventral cornuae, the latter being connected by a transverse ventral arch, while a dorsal arch connects the

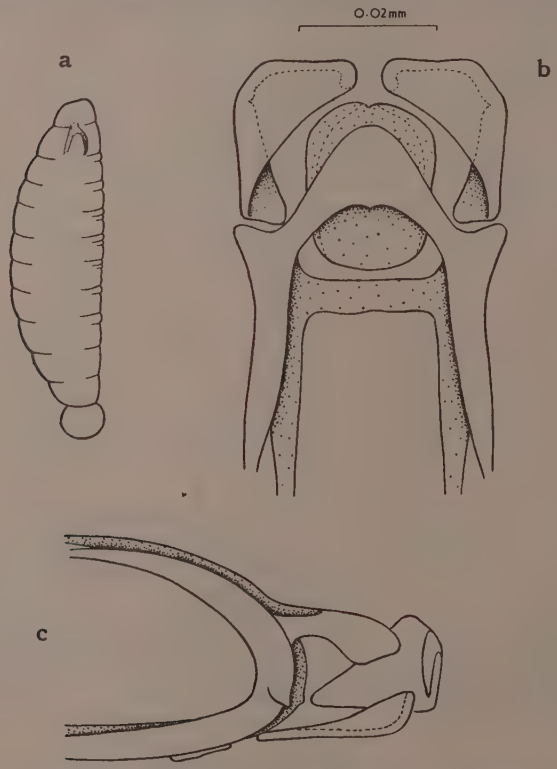

Fig. 8.—*Dorilas mauritianus* Hardy. (*a*) Early first larval instar. (*b*)–(*c*) Buccopharyngeal armature of same, dorsal and lateral aspects, respectively. (In (*c*), the left lateral sclerite is omitted).

dorsal cornuae near their bases and projects well forwards. Articulated to the basal piece are two lateral sclerites which curve sharply inwards and bear a large, sharp, downwardly projecting tooth at their tips. A median ventral sclerite, with thickened lateral edges, articulates with the ventral arch of the basal piece.

Two cup-like, sclerotised, depressions, presumably sense organs, are present on the head segment, one on each side of the mouth.

(ii) *The Second Larval Instar.*

When mature, this stage is robust and about 2·5 mm. long after killing in alcohol. Segmentation is obscured by the intricate folding of the integument (fig. 9*a*). The posterior vesicle is well developed.

The tracheal system is amphipneustic and the tracheal trunks are connected by large anterior and posterior transverse commissures. Both anterior and posterior spiracles are elevated. The anterior spiracles (fig. 9*b*) each have three or four openings and the walls of the atrium are developed into projections

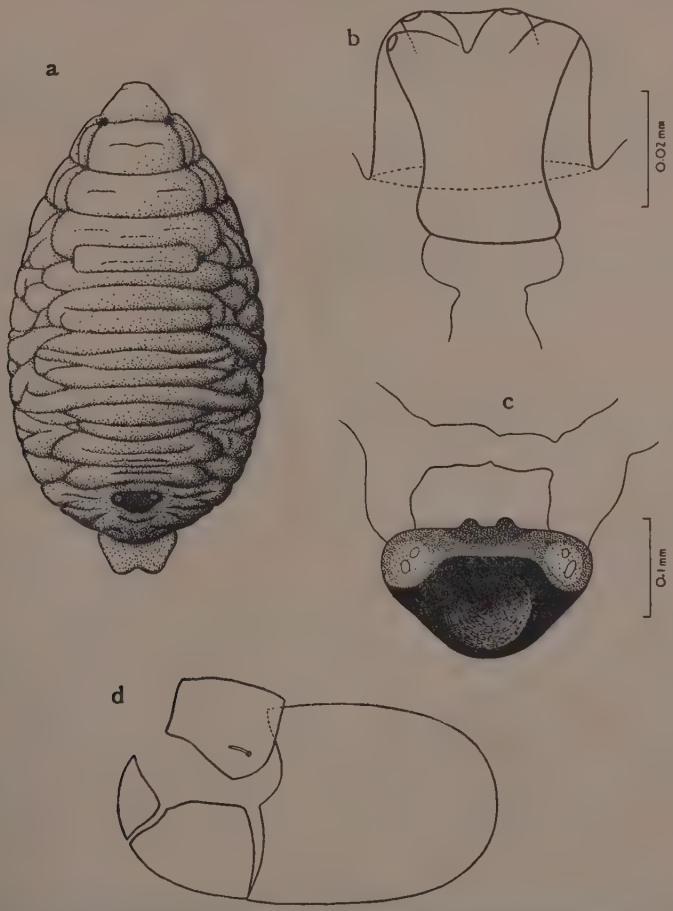

Fig. 9.—*Dorilas mauritianus* Hardy. (*a*) Mature second larval instar. (*b*) Anterior spiracle of same. (*c*) Posterior spiracles and spiracular plate of same. (*d*) Empty puparium.

to form a baffle (not shown in the figure). The posterior spiracles (fig. 9*c*) are borne on a thickened plate and each has two or three openings. The atrium of each of the posterior spiracles is also developed into a complicated baffle chamber. The spiracular plate is very heavily sclerotised and has a funnel-like depression, the point of which tapers into the body. Two projections at its anterior edge also taper into the body.

The mouth parts of this instar are obscure. The basal piece is massive and triangular in shape when viewed from the side; ill-defined lateral arms project forwards. Two lightly sclerotised ventral sclerites are discernible and they terminate anteriorly in forwardly directed spines.

Four distinct, bulbous, appendages, probably antennae and palps, are present near the mouth.

(iii) *The Puparium.*

The puparium is 2·6–3·0 mm. long. Its surface is finely granulate and of a reddish-brown colour when fresh but darkens after about two days until it is virtually black. The small, slender, prothoracic cornicles of the pupa project through round holes in the puparium.

The anterior portion of the puparium is forced off during emergence of the adult and is broken into pieces along definite lines of fracture. Figure 9*d* shows the anterior portion fractured into three pieces but sometimes the small anterior fragment is not detached and remains as part of the ventral fragment. The dorsal fragment carries the prothoracic pupal cornicles.

(*b*) The life cycle.

The adults are small, dark, inconspicuous flies and in flight they weave and hover among the cane shoots. They are exceedingly difficult to collect for, although their flight is rather slow, nets can seldom be used effectively in the densest cane growth where they usually pursue their erratic and elusive course. They were sometimes seen feeding upon honey-dew dropped by the cane aphid, *Longiunguis sacchari* (Zehnt.), but attempts to attract them by scattering drops of sugar and honey solutions on cane leaves were not successful.

Reference is made to Jenkinson (*quoted in* Perkins, 1905*b*) and Williams (1910, 1913) for some account of the oviposition behaviour of Pipunculid flies. Oviposition of the species under consideration was not observed but the hosts are attacked in the nymphal stage, for larvae were found in the third, fourth and fifth nymphal instars. The first and second nymphal host instars were not found to be attacked but only a few of these forms were dissected. Nearly all the larvae found in adult hosts were well developed but a few contained very small first instar larvae. Oviposition into adult hosts may therefore occur but it is clear that hosts are normally in the nymphal stage when attacked.

There are only two larval instars and larval development is completed only after the host has moulted to the adult stage. The young larva is free in the cavity of the host's abdomen and has no particular orientation. Later, when it is larger and fills much of the abdominal cavity, it lies with its body in the same direction as that of its host, with either the head or the tail forward. According to Kellin and Thompson (1915), the first instar larva of *Ateleneura aperta* Meig. almost invariably has its head forward (*i.e.* towards the host's

thorax) and the second instar larva lies in the opposite direction. Perkins (1905*b*), on the other hand, states that mature larvae of *Pyrpaeolus* spp. nearly always lie with the head forward. The larva of the Mauritian species, before moulting, usually lies with its head forward but the mature larva is orientated in either direction with about equal frequency.

The mature larva virtually fills the abdomen of the adult host, which appears somewhat distended, and emerges from it by splitting the integument across the dorsal surface between two segments, usually between the third and fourth. The host is, of course, killed. Pupation seems to occur in the soil for puparia were never found on shoots of leafhopper infested cane. The duration of the pupal stage in the laboratory was 23 days (seven puparia : December).

All parasitised hosts which were dissected (about 80 nymphs and 90 adults of either *Perkinsiella* or *Dicranotropis*) contained only one larva. No remains of dead larvae were found, and it therefore appears that either the adults do not oviposit into hosts already attacked or, if they do, the eggs, or the larvae immediately after hatching, fail to develop. Kelin and Thompson (1915) sometimes found two larvae of *Atelenevra* in the same host although only one ever reached maturity.

(*c*) The effects of parasitism upon the hosts.

Apart from causing the untimely death of the adults, parasitism affects the genitalia and the sex organs of the hosts in a manner not dissimilar from that of *Elenchus*. Aberrant genitalia occur in a proportion of parasitised leafhoppers (Table VI), presumably in those which were attacked early in the nymphal stage. The aberrations in both *Dicranotropis* and *Perkinsiella* are similar to those which, in the former, result from sybopisation.

The sex organs of parasitised leafhoppers of both sexes were either completely absent, as far as could be determined by careful dissection, or they were reduced to various extents. Attacked females were never found with mature eggs and, when the organs were present, the ovarioles were either empty or rudimentary (fig. 10). The sex organs of attacked male leafhoppers were not always distinctly affected, and the influence of the parasite was not more pronounced on one part of the male reproductive system than on another, as is the case on the ovaries of female hosts.

The effect of parasitism by *Dorilas* upon the sex organs of female hosts is more extreme than that which results from sybopisation, when the ovaries are often functional for a while before they atrophy. The difference results from the fact that nearly all hosts attacked by *Dorilas* commence adult life with a parasite larva already well developed and which matures rapidly. In the very few adult hosts found with small larvae, the ovaries were devoid of mature eggs and, as it seems doubtful if larvae of such small size could yet have affected the host, it is probable that the hosts were freshly moulted and that the larvae originated from eggs deposited into the host just before its final moult. The stages of *Elenchus* present in young sybopised adult hosts are various, triungulins only may be present or there may be advanced larvae, and the state of the ovaries and their ability to develop mature eggs varies accordingly.

It is very noticeable in hosts attacked by *Dorilas* or *Elenchus* that the effect of parasitism on the sex organs is most pronounced in female hosts. This is accounted for by the considerable sustenance needed by the ovaries of a freshly

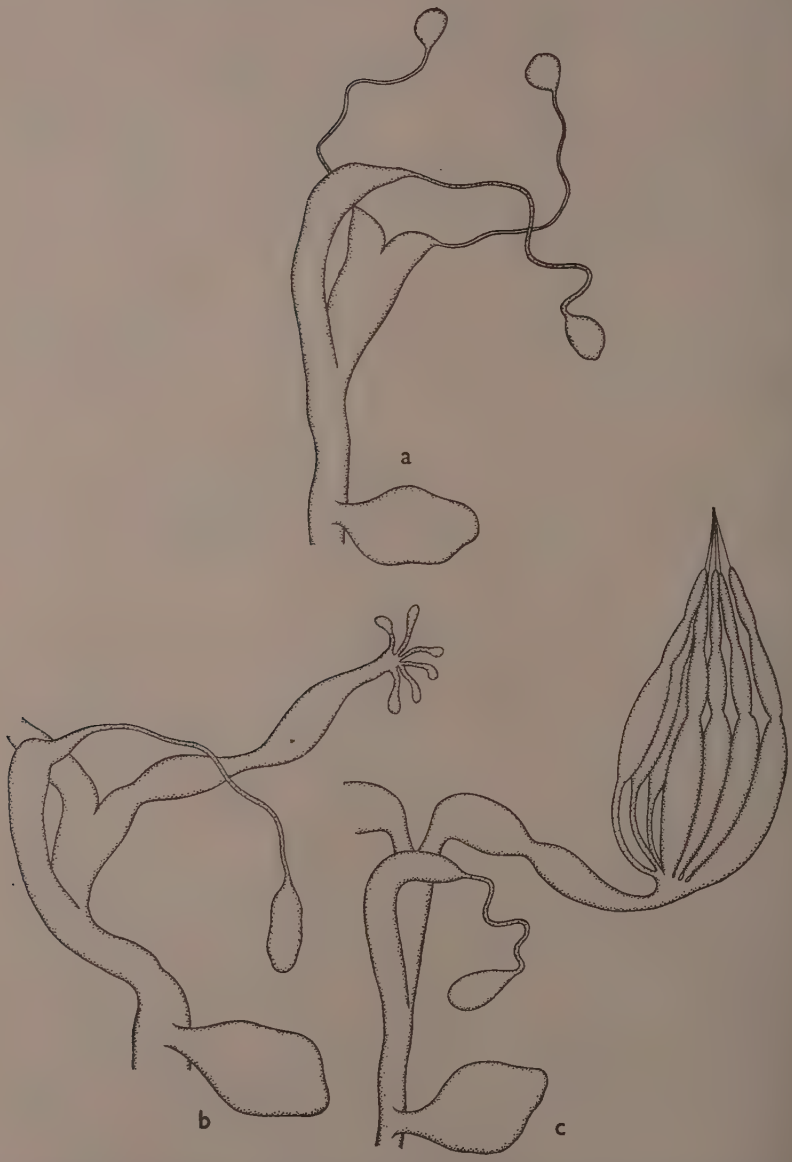

Fig. 10.—(*a*)–(*b*) Examples of reduced reproductive systems in female *Dicranotropis* following parasitism by *Pipunculus*. (*c*) A normal reproductive system for comparison.

moulted adult in order to develop mature eggs and later to continue their production. The male organs need comparatively little sustenance in adult hosts. The drain upon the body nutrients caused by parasites is thus reflected most by the state of the ovaries.

(*d*) Parasitism in the field.

Table IX shows the percentage parasitism, assessed by dissection, of field-collected samples of nymphal and adult *Dicranotropis* and *Perkinsiella*. With one exception, all the samples were taken in the same field where the leafhoppers were relatively numerous.

TABLE IX.—*Parasitism by* Dorilas *of field-collected nymphal and adult leafhoppers.*

(a) *D. muiri.*

		4th and 5th instar nymphs.			Adults.		
Locality.	Date	Number collected.	Number parasitised.	% parasitised.	Number collected.	Number parasitised.	% parasitised.
Flacq .	8.viii.55	13	1	7·7	.	.	.
„ .	16.ix.55	12	5	41·7	123	4	3·3
„ .	22.ix.55	39	10	25·6	.	.	.
„ .	26.ix.55	29	8	27·6	.	.	.
„ .	4.x.55	12	5	41·7	144	28	19·4
„ .	7.x.55	16	6	37·5	81	17	21·0
„ .	4.xi.55	.	.	.	46	6	13·0
Totals . . .		121	35	28·9	394	55	13·9

(b) *P. sacchariciда.*

		4th and 5th instar nymphs.			Adults.		
Locality.	Date.	Number collected.	Number parasitised.	% parasitised.	Number collected.	Number parasitised.	% parasitised.
Constance	22.vii.55	12	3	25·0	160	14	8·75
Flacq .	8.viii.55	117	37	31·6	100	5	5·0
„ .	16.ix.55	.	.	.	50	2	4·0
„ .	14.x.55	.	.	.	50	5	10·0
„ .	14.xi.55	.	.	.	100	7	7·0
Totals . . .		129	40	30·2	460	33	7·2

It will be seen from the data in the tables that nymphs were much more highly parasitised than adults. This is attributed to the virtual (if not complete) absence of attack on adult leafhoppers and to the early death of the adults which were parasitised as nymphs. A disproportionate number of the adult leafhoppers collected were therefore survivors. The value of *Dorilas* as an agent of natural control is, therefore, underestimated if parasitism of adult leafhoppers only is assessed. As the parasite does not cause nymphal mortality, the percentage parasitism of the last instar nymphs gives a fairly good estimate of the proportion which will succumb after moulting to the adult form. The majority of the nymphs which were collected were in the fifth instar but some,

particularly those in the fourth instar, would have been liable to further attack if left in the field. The data in Table IX are, however, sufficient to show that a high mortality of both *Dicranotropis* and *Perkinsiella* can result from attacks of *Dorilas*.

TABLE X.—*Parasitism by* Dorilas *and* Elenchus *of field-collected samples of adult* Dicranotropis.

(Data abstracted from Tables VII and IX).

Locality.	Date.	Number collected.	% parasitised. By *Elenchus*.	% parasitised. By *Dorilas*.	% overall parasitism.
Flacq .	16.ix.55	123	59·3	3·3	62·6
,, .	4.x.55	144	43·8	19·4	63·2
,, .	7.x.55	81	39·5	21·0	60·5
,, .	4.xi.55	46	45·7	13·0	58·7

Some of the data in Tables VII and IX may be combined, where they relate to the same collections, to show the total estimated parasitism of adult *Dicranotropis* by *Dorilas* and *Elenchus*. This has been done in Table X. It has already been remarked that multiparasitism by these parasites does not normally occur in *Dicranotropis*. The above remarks concerning estimates of parasitism of adult hosts by *Dorilas* should be borne in mind when examining Table X.

7. Spiders.

Salticid spiders were seen to feed upon *Dicranotropis* and *Perkinsiella* on a few occasions. Spiders of various kinds abound in sugar-cane fields but, as they feed upon a variety of insects, it is difficult to judge their importance as enemies of any particular insect species. The author is inclined to believe that their importance as natural enemies of the cane leafhoppers is not inconsiderable.

8. The Interrelations of the Natural Enemies and their Hosts.

With the exception of *Elenchus templetoni*, all the natural enemies which have been considered parasitise successfully both *Perkinsiella* and *Dicranotropis*. The following list summarises their direct effect upon the two leafhoppers.

Natural enemy.	*Effect upon the hosts.*
Ootetrastichus pallidipes, *Paranagrus optabilis*, *Anagrus flaveolus*	Egg mortality.
Pseudogonatopoides mauritianus	Nymphal mortality.
Spiders	Nymphal and adult mortality.
Dorilas mauritianus	Sterility or reduced fertility of adults and their early death.
Elenchus templetoni	Nymphal mortality, sterility or reduced fertility of adults and probably their premature death also (*Dicranotropis* only).

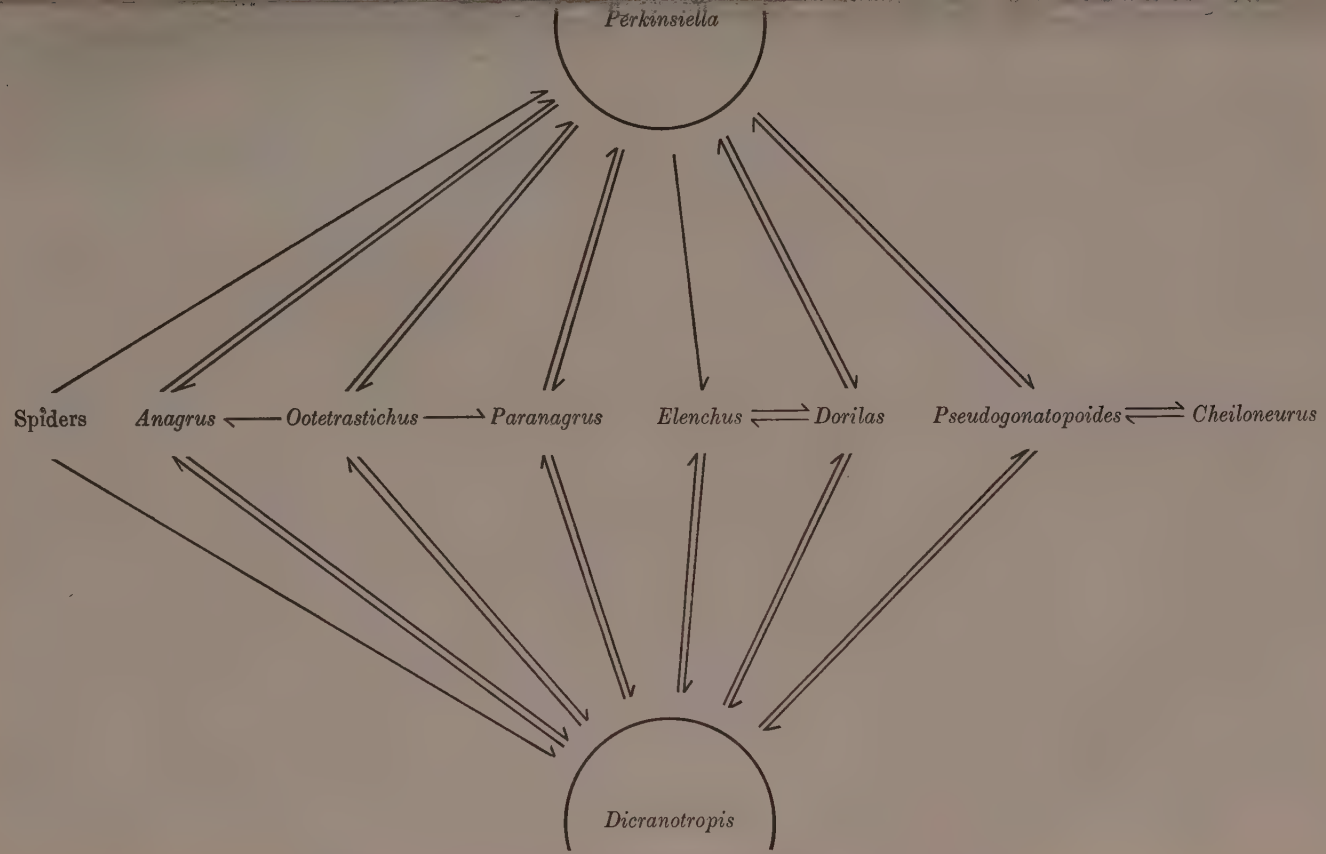

FIG. 11.—The interrelations of the sugarcane leafhoppers and their parasites.

Figure 11 illustrates the interrelations between *Dicranotropis*, *Perkinsiella* and the above natural enemies. It illustrates, above all, that the epidemiology of the two leafhoppers, which co-exist in cane fields, is a single study. The population of one is conditioned by the population of the other owing to the natural enemies which they have in common.

Of the various parasites, *Anagrus* seems only to attack the cane leafhoppers incidentally and is primarily a parasite of the maize leafhopper, *Peregrinus*.

Ootetrastichus and *Paranagrus* are both common parasites of *Perkinsiella* and *Dicranotropis* whenever their eggs are numerous. It is not known if super- or multiparasitism occurs within the host eggs but the final larval stage of *Ootetrastichus*, after leaving the egg in which it developed, often preys indiscriminately upon healthy and parasitised host eggs and may also destroy pupae of its own kind. This parasite is, therefore, responsible for mortality of *Paranagrus*, *Anagrus* and of its own immature forms. On the other hand, the parasite may likewise destroy several healthy host eggs during its development.

Pseudogonatopoides, which attacks and destroys the nymphs, seems too rare to be of importance as a control agent. Its rarity may be due to the hyperparasite, *Cheiloneurus*. Scarcity of material precluded observations on the interrelations of *Pseudogonatopoides* with *Dorilas* and *Elenchus*.

Dorilas and *Elenchus* are sometimes abundant parasites of the nymphs and adults. The interrelations between them and their hosts are complicated. The triungulins of *Elenchus* readily attack *Perkinsiella*, but the larvae to which they give rise almost invariably fail to develop to any extent and their dead, shrunken, bodies accumulate in the host's abdomen. *Perkinsiella* is apparently unaffected by this abortive stylopisation. The presence of *Perkinsiella* has, however, an adverse effect upon *Elenchus* by the removal of triungulins which might otherwise have encountered a suitable host, i.e. *Dicranotropis*.

In *Dicranotropis*, multiparasitism occurs in the form of *Dorilas* larvae and triungulins of *Elenchus* in the same individual. *Dorilas* larvae were not found to accompany other stages of *Elenchus* unless these had completed development or died. Only two examples of this were found. The first was an adult *Dicranotropis* containing a small first instar *Dorilas* larva and bearing an empty puparium of *Elenchus* ; the second, also an adult, contained, in addition to a small *Dorilas* larva, two puparia and an adult female of *Elenchus* which were unextruded and therefore dead or dying. It is concluded that triungulins cannot develop when they enter hosts already attacked by *Dorilas* and, conversely, *Dorilas* cannot parasitise hosts with living *Elenchus*. It might also be noted here that never more than one *Dorilas* larva was found in a host and in no instance was a dead larva found. Thus, either the female *Dorilas* refrains from ovipositing when it encounters a host containing living *Elenchus* or a larva of its own kind, or its eggs, or its larvae immediately after hatching, fail to develop.

Stylopisation of *Perkinsiella* does not seem to affect *Dorilas* in any way owing to the physiological unsuitability of this host for the development of *Elenchus*. A *Dorilas* larva in *Perkinsiella* is frequently accompanied by both triungulins and the larvae of *Elenchus*. Usually the *Elenchus* are dead but in some hosts one or two may seem alive (since live *Elenchus* larvae were never seen to move, dead larvae could be distinguished as such only if their bodies had begun to blacken and shrink). The dead *Elenchus* clearly do not affect

parasitism by *Dorilas* and neither, apparently, do those which, though seemingly alive, are fated to die.

V. Discussion of the Factors Governing Population Densities.

The factors controlling population density fall into two groups, the intrinsic and the extrinsic factors. The former concern the inherent abilities of the species to multiply and survive (their biotic potential). The latter include biotic and abiotic factors of the environment which may favour either increase or decrease of the populations. Only the extrinsic factors, as far as they are known, are considered here.

The abundance of the leafhoppers, locally and generally, in the island has already been described. Their populations are generally so low as to attest a considerable environmental resistance. The interest of the extrinsic factors governing their population densities therefore centres upon assessing which factor or factors are responsible for this high environmental resistance.

Sugar-cane in Mauritius is cultivated extensively and covers a large part of the island. There is virtually no crop rotation and the same lands are under sugar-cane year after year. Further, the harvesting period extends over about five months and fields are ratooned for five or six years before replanting. Consequently, there is no time of the year when cane growth is unavailable to the leafhoppers and the acreage under sugar-cane is more or less constant in its extent and location. The continuity and the quantity of food and shelter available to the leafhoppers are, therefore, not limiting factors.

The various vegetative states of sugar-cane, due to different varieties of cane and to growth, offer a certain limited variety of habitats, some of which are preferred by the leafhoppers, or which perhaps favour their increase, more than others. The effect upon the density of leafhopper populations is, however, not considerable and seems to amount to no more than a tendency for more or for fewer leafhoppers to be associated with vegetative growth of any given type. This factor is unable to account for the low general populations of the leafhoppers.

Climatic and seasonal variations within the island, as already stated, do not have any pronounced effect upon the populations of the two leafhoppers and there is no reason to suppose that the climate is generally adverse. Dispersion is influenced by seasonal and weather factors which affect, respectively, the incidence of macropterous adults and their readiness to fly.

The effects of the various natural enemies have been described in the preceding sections and only their general role upon populations of the leafhoppers remains to be considered. It is rarely possible in practice to obtain more than a rough appreciation of the importance of natural control in an insect population. Notable exceptions are when biological control of an insect pest is quickly achieved following introduction into a country or area of parasites or predators which were previously absent. The obvious reduction of the pest population and the diminished economic losses then provide incontrovertible evidence of the efficacy of natural control. When such evidence is not available, as in stable or settled associations of phytophagous and entomophagous insects, the role of natural enemies is not easily assessed, particularly if the associations are complex, and field data, quantitative or otherwise, can do little more than guide the observer to a general appreciation of the importance of natural control. Simmonds (1948) has discussed some of the difficulties of determining

the value of parasitic control. The role of predators is equally difficult to assess. When a pest population is low, however, a very considerable handicap is the difficulty of collecting sufficient samples, or of making sufficient observations, to generalise with confidence upon the individual or combined value of entomophagous species as control agents. Under such circumstances, and if there is an absence of other effective controlling factors, the mere presence of a variety of natural enemies is strong evidence for the efficacy of natural control.

The field studies on *Perkinsiella* and *Dicranotropis* were considerably handicapped by their low populations and further by their secretive habits. The quantitative data upon parasitism which has been presented is not considerable and relates only to *Elenchus* and *Dorilas*. However, it is shown that when the leafhoppers are relatively numerous, a high degree of attack by these parasites may occur, while observations also showed *Ootetrastichus* and *Paranagrus* to be very common parasites. This, in conjunction with the occurrence of other parasites and predators, the low leafhopper populations, and the apparent absence of other effective controlling factors, offers considerable support for the conclusion that a high degree of natural control exists and is the chief factor governing population densities of *Perkinsiella* and *Dicranotropis*.

VI. Summary.

1. There are two species of Delphacidae which breed upon sugar-cane in Mauritius. These are *Perkinsiella saccharicida* Kirkaldy and *Dicranotropis muiri* Kirkaldy. Adults of *Peregrinus maidis* (Ashmead) are also sometimes found on sugar-cane but these are strays.

2. The history, biology, bionomics and economic importance of *P. saccharicida* and *D. muiri* in Mauritius are described and discussed. Their immature stages, and also those of *P. maidis*, are described.

3. Both *P. saccharicida* and *D. muiri* occur generally on sugar-cane in the island but their populations are low and they cause no apparent direct injury to cane growth. The former is, however, a vector of Fiji Disease of Sugar-cane which does not, as yet, occur in Mauritius.

4. The factors which affect the population densities of *P. saccharicida* and *D. muiri* are considered. Natural enemies are numerous and it is concluded that they are primarily responsible for the low general level of the leafhopper populations. The same parasites attack both species of leafhopper and the interrelations between the parasite and host populations are complex. The two hosts and their enemies constitute a fairly distinct biological association in sugar-cane fields.

5. The natural enemies of *P. saccharicida* and *D. muiri* in Mauritius are the following: *Ootetrastichus pallidipes* Perk. (Eulophidae), *Paranagrus optabilis* Perk. (Mymaridae), *Anagrus flaveolus* Waterh. (Mymaridae), *Pseudogonatopoides mauritianus* Williams (Dryinidae), *Elenchus templetoni* Westw. (Elenchidae), *Dorilas mauritianus* Hardy (Pipunculidae) and several species of spiders. *Cheiloneurus gonatopodis* Perk. is a secondary parasite through *P. mauritianus*.

E. templetoni and *D. mauritianus* are considered in some detail and descriptions of their stages are included. The former is the only parasite which is unable to develop in both hosts. In *P. saccharicida*, which it readily attacks, the larvae invariably fail to complete normal development.

VII. Acknowledgments.

The author is indebted to Dr. W. J. Hall, Commonwealth Institute of Ento-

mology, for his encouragement, for supplying photostats of papers which otherwise were unobtainable, and for assistance in identifying several of the species involved. Dr. C. E. Pemberton, formerly entomologist to the Hawaiian Sugar Planters' Association, and Mr. D. T. Fullaway, Hawaiian Board of Agriculture and Forestry, kindly confirmed the identity of *Ootetrastichus pallidipes* Perk. by reference to the types. Mr. C. Mongelard, formerly of the Department of Agriculture, gave the author much assistance in the laborious task of collecting leafhoppers in the field.

The work was done under the general direction of Mr. M. N. Lucie-Smith, Director of Agriculture, Mauritius.

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